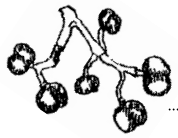
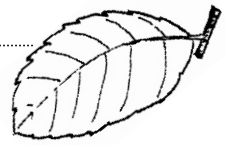


Impact of forest fragmentation and disturbance on the endangered tropical tree *Prunus africana* (Rosaceae)



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CONTENTS

1 SUMMARY

Anthropogenic forest fragmentation and disturbance imperil the survival of species and have been shown to affect ecological processes and communities. Moreover, they cause plant species to suffer from genetic drift and inbreeding, which affects population viability negatively. To assess the impact of fragmentation and disturbance on biodiversity and ecosystem processes I investigated (i) the frugivore community together with its seed dispersal service for *Prunus africana* (Rosaceae), (ii) the small mammal activity in combination with seed predation rates of the focal tree and (iii) the genetic structure of adult in comparison with seedling populations using microsatellite markers in Kakamega Forest, western Kenya. Comparing adults with seedlings allowed studying changes in gene flow between generations with adults reflecting the pattern before and seedlings after forest fragmentation. During the frugivore census within the forest I recorded 49 frugivorous species (birds and monkeys) and observed 36 of them feeding on *P. africana* fruits. Even though the overall species richness of the forest declined marginally significantly from main forest to fragmented sites I recorded slightly higher numbers of frugivores in *P. africana* trees in fragments. Overall species richness was higher in highly than in less disturbed sites and concordantly species richness increased significantly in *P. africana* trees in highly disturbed sites. Correspondingly, seed dispersal was marginally significantly higher in fragmented than in main forest sites and in highly compared to less disturbed sites. These results suggest that the quantity of seed dispersal seems to be slightly enhanced in fragments and highly disturbed sites, indicating a certain species redundancy in an ecosystem which may compensate loss of single species. Small mammal activity was existent throughout the entire forest and terrestrial predation of *P. africana* seeds was mainly caused by one rodent species (*Praomys* cf. *jacksonii*). Activity of seed predators tended to be higher in highly disturbed compared to less disturbed sites. Moreover, I recorded significantly higher predation rates for single seeds in contrast to groups of seeds of *P. africana* in highly compared to less disturbed sites. Thus, the two studied processes in the life cycle of *P. africana* revealed to some degree contrasting results demonstrating that extrapolation from one process in the life cycle of a tree to another is not possible. Genetic differentiation of adult tree populations was low (F_{ST} = 0.026) with ~ 97 % of the variation

within populations, reflecting extensive gene flow in the past. However, genetic variation of seedlings was slightly higher ($F_{ST} = 0.086$) with ~ 91 % of the variation within populations. Additionally, for seedlings, but not for adults, I recorded an isolation by distance (IBD) pattern. Thus, the increased genetic differentiation combined with the IBD-pattern for seedlings are first indicators for restricted gene flow in the seedling stage class as a result of forest fragmentation. Even though the observational data showed no decline in seed dispersal as a result of fragmentation, the genetic results demonstrated already decreasing genetic exchange between populations. Thus, genetic data provide an important indicator for long-term changes in ecosystems whereas field data reveal only snap-shots. To conclude, fragmentation and disturbance affect genetic diversity, ecosystem processes and species diversity in variable ways, respectively. Therefore, future studies should consider different diversity levels to evaluate consequences of human impact.

2 GENERAL INTRODUCTION

Worldwide loss of biodiversity has increased dramatically during the past few decades (Ehrlich and Wilson 1991, Soulé 1991). The broad spectrum of human activities, e.g. habitat destruction, alteration, fragmentation and disturbance, threatens complete ecosystems (Primack 1993). Especially in tropical forests diversity decline appears to be extremely rampant. Consequences of human impact comprise decline of species diversity (Kattan et al. 1994, Kruess and Tscharntke 1994, Loreau et al. 2001), decrease of genetic diversity (Young et al. 1996, Keller and Waller 2002) and modification of ecological processes and services (Chapin et al. 2000, Luck et al. 2003, Şekercioğlu et al. 2004). However, consequences for ecosystem functioning are hardly investigated (Tilman 1999, Loreau et al. 2002, Larsen et al. 2005).

The loss of keystone species or mobile link organisms such as pollinators and seed dispersers may have far-reaching consequences for plant communities (Lundberg and Moberg 2003) such as decreased pollination and in turn seed output (Aizen and Feinsinger 1994) or reduced seed removal (Cordeiro and Howe 2003). In addition, the disruption of habitats might amplify these consequences in terms of increased predation rates (Santos and Tellería 1994), diminished recruitment (Cordeiro and Howe 2001, 2003) and genetic isolation (Aldrich and Hamrick 1998). Therefore, determining how biodiversity dynamics and ecosystem processes interact in the face of human impact, i.e. fragmentation and disturbance remains a challenge.

2.1 Consequences of fragmentation and disturbance for seed dispersal

In tropical forests more than 90 % of all tree species rely on animals as dispersal agents (Howe and Smallwood 1982). Thus, seed dispersal by animals is a particularly crucial service. Fruit-eating birds and mammals profit by dispersing the seeds in the form of nutrition. Since frugivorous animals are the dominating vertebrate group in tropical forests, it is a challenge for them to find fruiting trees and with it the fleshy fruit reward (Howe and Westley 1988). Consequently, fruit availability is one crucial factor influencing the frugivore community (Howe and Estabrook 1977, Thomson and Willson 1979). Figs as keystone species, for instance, have been shown to provide fruits in scarce fruiting times for the survival of frugivore communities (Bleher et al. 2003).

Seed dispersal can have different benefits to tree species. Dispersed seeds may escape from the area of "chemical influence" of the parent plant, from the high-density concentration of competing siblings and from natural enemies such as pathogens, herbivores or seed predators. Moreover, seed dispersal may be advantageous through colonization of vacant, favourable microsites and result in a higher seedling establishment and seedling survival away from the crown (Janzen 1970, Howe and Smallwood 1982). This highlights the importance of seed dispersal as mutualistic ecosystem service for the persistence of tropical plant communities (Nason and Hamrick 1997).

Several studies have shown that fragmentation and human disturbance can lead to a decline of frugivores (Santos and Tellería 1994, Pizo 1997, Cordeiro and Howe 2003) or to alteration of their behaviour. Many forest species, for example, do not cross large gaps of deforested open landscape (Hannon and Schmiegelow 2002). Through selective logging of fruiting trees, frugivore diversity and abundance might decrease. Changes in the frugivore community may have consequences for animal-dispersed tree species and in turn their seed dispersal potential. Consequently, this loss of seed dispersers can lead to a reduced seed removal (Wright et al. 2000, Cordeiro and Howe 2003) and diminished regeneration (Wright et al. 2000, Cordeiro and Howe 2001, 2003). In the long-term, forest alteration might lead to a break-down of seed dispersal and establishment processes and may influence the regenerative potential of tree species (Bond 1995, Bleher and Böhning-Gaese 2001). Therefore, it is important to know in which way fragmentation and disturbance affect the ecosystem service of seed dispersal.

2.2 Consequences of fragmentation and disturbance for seed predation

Seed predation is thought to play a pivotal role for regeneration (Hulme 1994, 1996, Castro et al. 1999), colonization ability (Schupp et al. 1989, Myster and Pickett 1993) and spatial distribution (Hulme 1997, Forget et al. 1999) of trees. In tropical forests, tree species commonly suffer very high predation rates between seed fall and germination affecting their recruitment (Janzen et al. 1976, Howe et al. 1985, Schupp 1990). A combination of many different ecological, environmental and physiological factors determines predator activity and in turn seed survival.

Seed predators include insects as well as small and large birds and mammals. Some of these different predators may not only act as seed predators but as well as secondary seed dispersers and consequently either have a negative or positive impact on seeds (Forget 1996). Numerous field studies have shown that while seed and seedling survival away from adult specimens depends on the quality of microhabitats, mortality caused by terrestrial vertebrates is independent of the distance from the parent tree (Schupp and Frost 1989, Howe 1993). In response to seed predation many tree species have developed strategies to avoid being eaten such as masting, i.e. synchronous high seed production to saturate predators and to allow some seeds to survive (Silvertown 1980).

Habitat fragmentation and disturbance may modify the intensity of seed predation. The reduction and modification of an undisturbed continuous forest into small highly disturbed fragments may change the composition, abundance and distribution of seed predators (Sork 1987, Terborgh and Wright 1994). One consequence of fragmentation is the change of a former continuous predator habitat into islands. Below a certain threshold size of the fragment, decreased home ranges may lead to intensified foraging in a smaller spatial area and in turn enhanced predation pressure on seeds. While fragmentation results mainly in a decrease in size, disturbance modifies a former undisturbed habitat in many different ways. Selective logging, for instance, results in advanced light conditions and thereby in increased understory providing better protection of small mammals and birds against aerial predators (Kotler and Blaustein 1995) and hence enhanced seed predation pressure.

Several studies have shown that small mammal abundance increased as a result of fragmentation and disturbance (Laurance 1994, Santos and Tellería 1994, 1997). Such an increase in abundance of predators might explain the higher predation rates of seeds in these forest fragments (Santos and Tellería 1994). However, the abundance and diversity of

small mammals may also decrease with fragmentation and disturbance (Turner and Corlett 1996, Harrington et al. 1997), which could in turn account for reduced seed predation rates. Accordingly, fragmentation and disturbance may hamper forest regeneration by increasing the loss of individuals between the seed and seedling stage. Therefore, assessing the impact of fragmentation and disturbance upon seed predation is vital for the regeneration of tree species.

2.3 Consequences of fragmentation for the genetic structure of populations

Natural populations vary enormously in size and structure, and this has implications for their genetic composition. The genetic structure of plant populations is determined by the counteracting forces of mutation, genetic drift and gene flow via pollen and seeds (Hartl 1980). Mutation and drift may lead to genetic differentiation within and among plant populations whereas the gene flow vectors should lead to an exchange between different gene pools (Hamrick et al. 1993). Thus, the genetic structure depends on the frequency of gene flow by pollen and seed dispersal in populations (Shapott 1999).

Extensive pollen transport supposably results in genetic homogeneity among populations while reduced pollination likely causes decreased gene flow leading to considerable spatial genetic structure among populations (Ghazoul and Mcleish 2001, Cascante et al. 2002). The same pattern can be found for seed dispersal. Trees with extensive seed dispersal show little or no genetic structure among populations (Knowles 1991, Xie and Knowles 1991), whereas trees with limited seed dispersal show more obvious genetic structure among populations (Perry and Knowles 1991, Leonardi and Menozzi 1996, Ueno et al. 2000). While pollination only occurs between already established populations, seed movement can also result in colonization of new environments. Therefore, pollination always leads to a homogenization of the gene pool, whereas gene flow via seed dispersal can result either in a homogenization of the gene pool in cases it occurs between established populations (Slatkin 1977) or to a differentiation of the gene pool in case of a colonization event (Wade and McCauley 1988), where most likely only a few seeds reach the new site.

Genetic variation is likely to be crucial in the long-term, providing evolutionary potential of populations. Low levels of genetic diversity may interact with other factors such as demographic and environmental variation and imperil the adaptive potential and fitness of populations. As a consequence, low levels of genetic diversity might lead to a

genetic bottleneck of a population or to extinction of a population or even an entire species (Gilpin and Soulé 1986, McLaughlin et al. 2002).

Habitat fragmentation, i.e. the reduction of large, continuous habitats to small, isolated remnants might function as a barrier for gene flow in natural populations. Often, decreased interfragment gene flow cannot compensate for rising levels of genetic drift as subpopulations become smaller and more isolated (Slatkin 1987, Hall et al. 1994). Trees are long-lived species with overlapping generations. This means that barriers for gene flow of e.g. the last 100 years are very hard to identify since genetic structure of adults probably pre-dates fragmentation. Additionally, it may take several generations until changing gene flow can be traced in the genetic structure. Decreasing gene exchange from adult trees to seedlings or saplings has been demonstrated as a result of fragmentation (Aldrich et al. 1998, Dayanandan et al. 1999). Therefore, comparing different stage classes such as adults with seedlings or saplings represents a possibility to detect genetic differences among forest remnants and to reveal the present pattern of gene flow.

2.4 Aims of the thesis

In this thesis I studied the consequences of anthropogenic forest fragmentation and disturbance for biodiversity, processes and services in the tropical Kakamega Forest, western Kenya. Kakamega Forest was a suitable study area for this question since it consists of a main forest block and surrounding fragments which allows a comparison between these two categories. Moreover, the extent of human disturbance varies throughout the forest as a result of different management policies of the Kenya Wildlife Service (KWS) and the Forestry Department (FD). The parts which are managed by KWS show lower levels of disturbance mainly connected with low numbers of logged trees whereas the parts managed by FD show higher extents of human disturbance in terms of high numbers of stumps. The endangered tropical tree species *Prunus africana* (Rosaceae) proved to be a suitable focal species because of its abundance throughout the whole forest and by producing animal-dispersed fleshy fruits.

The first aim of my thesis was to study the impact of fragmentation and disturbance on avian diversity and seed dispersal. The second aim was to investigate the effect of fragmentation and disturbance on seed predator activity and seed predation rates. The third aim was to determine the consequences of fragmentation for the genetic structure of populations. All three parts were performed in the main forest and in several surrounding

forest fragments to test for a fragmentation effect. Concerning the first two aims, I also tested for a disturbance effect between less and highly disturbed sites.

This thesis consists of three major chapters (chapter 3 to 5) which can be read independently. Each chapter is organized like a journal publication containing an introduction, followed by a methods, results and discussion section and by a short summary. The thesis closes with general conclusions including the deliverables of all three chapters.

The first major chapter (chapter 3) deals with the impact of fragmentation and disturbance on the overall frugivore community of the forest and in particular the frugivore community of the focal tree species *P. africana* and its seed dispersal. On the one hand I quantified the overall frugivore community of the forest as an indicator for species diversity. On the other hand I determined the frugivore assemblage on 28 fruiting *P. africana* trees, estimated seed dispersal, crop size and the general fruit availability of surrounding trees. Moreover, I considered the forest dependency of the species.

In the second major chapter (chapter 4) I focused on the effects of fragmentation and disturbance for seed predator activity and predation rates of *P. africana*. I quantified the activity of small mammals using Sherman-traps, identified potential seed predators through feeding experiments and performed predation experiments with single and groups of *P. africana* seeds.

The third major chapter (chapter 5) treats of the consequences of fragmentation for the genetic structure of *P. africana* populations. I examined the genetic structure of 93 adult trees and 58 seedlings in different fragments and the main forest using six microsatellite markers. Considering adults and seedlings allows studying changes in the gene flow pattern between generations before and after fragmentation.

3 CONSEQUENCES OF FRAGMENTATION AND DISTURBANCE FOR SEED DISPERSAL

3.1 Introduction

Tree populations in the tropics are currently threatened by destruction, fragmentation and degradation of forests (Turner and Corlett 1996, Whitmore 1997, Laurance et al. 2000). Responses of plants and animals to fragmentation and disturbance are highly variable, depending on species' characteristics and on the particular level of fragmentation and disturbance involved (Charlesworth and Charlesworth 1987, Kruess and Tscharntke 1994, Santos and Tellería 1994, Cole et al. 1995). The long-term consequences of fragmentation and disturbance for key ecosystem processes such as pollination and seed dispersal are hardly understood, despite their importance for conservation (Didham et al. 1996).

Frugivore visitation of fruiting trees and dispersal of seeds in forests can influence the persistence of plant species (Nason and Hamrick 1997, Martinez-Garza and Gonzalez-Montagut 1999, Da Silva and Tabarelli 2000). At the same time, the presence of fruiting trees in forests influences the maintenance of frugivore communities (Levey 1988, Guindon 1996, Whitney et al. 1998). The relationship between fruiting plants and their dispersal agents might affect both, plant and frugivore communities in forest ecosystems (Howe 1984, Willson 1992, Santos and Tellería 1994, Da Silva et al. 1996, Cordeiro and Howe 2003). Thus, understanding the impact of forest fragmentation and disturbance on seed dispersal may be crucial for maintaining diversity of both, animal-dispersed plants and frugivores, in fragmented and disturbed landscapes (Restrepo et al. 1999, Githiru et al. 2002, Graham et al. 2002).

Existing studies on the consequences of forest fragmentation on seed dispersal showed that fragmentation can lead to a decline of dispersal agents (Santos and Tellería 1994, Pizo 1997, Cordeiro and Howe 2003). Woodland fragmentation in Spain resulted in a loss of avian frugivores on *Juniperus thurifera*, and an increase of seed consumption by small mammals, leading to reduced seed dispersal and seedling establishment (Santos and Tellería 1994). Pizo (1997) recorded a loss of avian frugivores on *Cabralea canjerana* due to fragmentation, a decrease of small mammals but an increase of terrestrial frugivorous birds having a negative impact on seedling establishment. Forest fragmentation in Tanzania led to fewer dispersal agents on the tree *Leptonychia usambarensis* and, as a consequence, a decline of juvenile recruitment (Cordeiro and Howe 2003). However, a study of Graham et al. (2002) comparing visitation rates in continuous forest and remnants in Mexico showed no consistent pattern for the two tree species *Dendropanax aboreus* and *Bursera simaruba*. Theses studies show that fragmentation does not only affect the species composition but furthermore ecosystem services such as seed dispersal.

In the present study, I investigated the consequences of fragmentation and, in addition, forest disturbance on the frugivore community of a Kenyan forest and focused especially on the endangered tree *Prunus africana* and its seed dispersal. Since forest fragmentation and disturbance may in particular alter the habitat of forest species I tested whether forest-dependent species were specifically affected. The study area was Kakamega Forest, an Afromontane rainforest consisting of a main forest block and several fragments with two different management regimes reflecting different levels of disturbance. The objectives of the study were, first, to test whether fragmentation or disturbance affected the species composition and abundance of the overall frugivore community of the forest. Second, I determined whether these two factors changed the frugivore assemblage feeding on *P. africana*. For both questions, I took into account the degree to which the species were dependent on forest. Since crop size and general fruit availability are known to influence frugivores, I additionally assessed whether crop size and fruit availability in the surrounding forest influenced the frugivores on *P. africana*. Third, I quantified seed dispersal and tested whether seed dispersal rates varied between differently fragmented and disturbed sites. Finally, I tested whether the results were influenced by spatial autocorrelation.

3.2 Material and methods

3.2.1 Study area

The study took place in Kakamega Forest, western Kenya (between latitudes 0°14' and 0°21' N and longitudes 34°47' and 34°48' E). Kakamega Forest is the eastern most relict of the Congo-Guinean rainforest belt and lies at an altitude of 1,500 to 1,700 m above sea level. Average annual temperature of the forest is between 10.6° and 27.7° C (Tsingalia 1990); annual precipitation averages 2,007 mm and is highly seasonal with a rainy season from April to November and a short dry season from December to March (as averaged from Forest Department records at Isecheno Forest Station from 1982 to 2001). The forest covers an area of 8,500 ha of a main forest block surrounded by five forest fragments of various sizes (130–1,400 ha), Malava and Kisere in the north, and Yala, Ikuywa and Kaimosi in the south (Fig. 3.1). I treat Yala and Ikuywa as two different fragments because they are separated by a road that divides the narrow corridor of trees still connecting the two fragments. The forest is surrounded by a densely settled agricultural area (600 people/km^2) (KIFCON 1994). The matrix habitat consists of small patches of fields such as sugarcane, maize, beans or tea interspersed by single large forest trees and small shrubs.

The extent of human disturbance in the forest has been quantified for different parts of the forest (Bleher et al., in press): the northern part of the main forest block and the fragment Kisere are managed by the Kenya Wildlife Service (KWS) showing lower levels of anthropogenic disturbance. The southern part of the main forest block, and the fragments Malava, Yala, Ikuywa, and Kaimosi are managed by the Forest Department (FD) showing higher extents of anthropogenic disturbance. High levels of disturbance in Kakamega Forest are mainly connected with high numbers of logged trees (Bleher et al., in press). Further information on the fragmentation and disturbance history of Kakamega Forest is given in Tsingalia (1990) and Mitchell (2004).

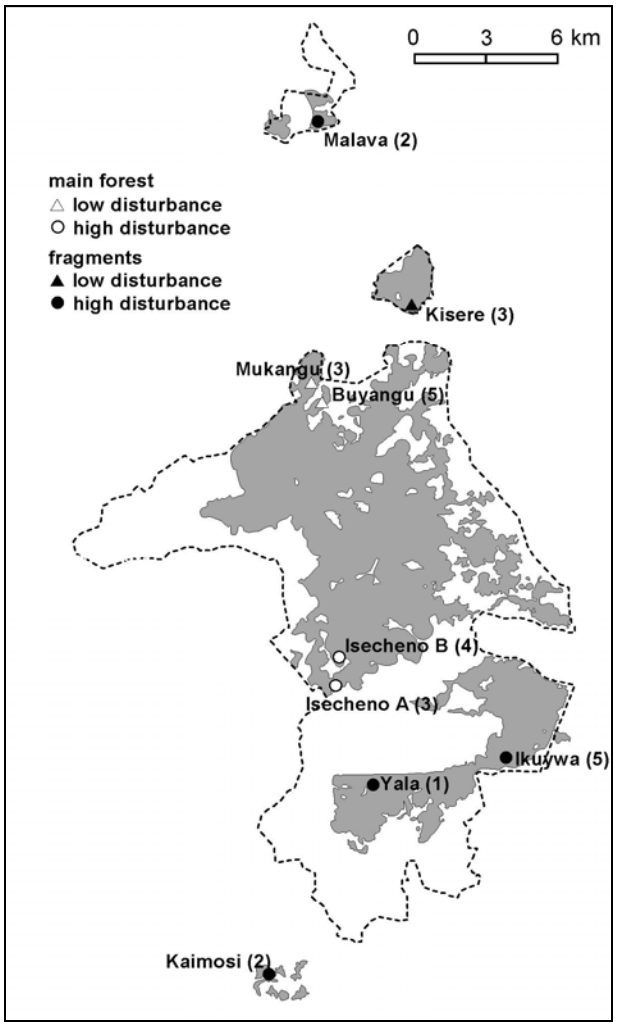


Figure 3.1: Map of Kakamega Forest and adjacent fragments with spatial position of the nine study plots. Numbers in parenthesis are numbers of observed trees per site. Triangles stand for less disturbed sites, circles for highly disturbed sites, open symbols for main forest sites and full symbols for fragments. Dashed line represents former forest boundary (1933), grey shading represents actual forest cover. Courtesy of G. Schaab.

3.2.2 Study species

Prunus africana Hook f. (Rosaceae) is an evergreen tree species typical of primary forests native to Africa and Madagascar. The monoecious tree grows up to 40 m in height producing small white flowers in elongated clusters and purple fleshy fruits (mean ± 1 *SD*, length: 9.3 ± 1.1 mm, width: 7.3 ± 0.8 mm, height: 7.0 ± 0.8 mm, mass: 0.4 ± 0.1 g, $N = 21$) with one seed (length: 8.1 ± 0.7 mm, width: 6.1 ± 0.4 mm, height: 5.5 ± 0.5 mm, mass: 0.15 ± 0.05 g, $N = 30$). Median crop size was 18,000 fruits per tree. The bark is medicinally used, the wood is durable and used for furniture (Cunningham and Mbenkum 1993, Schippmann 2001). Due to over-exploitation of wild populations the species has been listed in Appendix II of CITES (Cunningham and Mbenkum 1993, Schippmann 2001). A recent study on *P. africana* in the south of Kakamega Forest revealed a rapid decline of the population (Fashing 2004).

3.2.3 Overall frugivore community

I carried out a monthly census of the frugivore community from September 2001 to August 2002 in nine different plots of 1 ha with four plots in the main forest block (two in the south and two in the north) and five in fragments with one in each of the five forest fragments Malava, Kisere, Ikuywa, Yala and Kaimosi (Fig. 3.1). Although the plots appear to be situated at the edge of the main forest and the fragments (Fig. 3.1), all plots were placed at a distance of at least 100 m to the forest edge to avoid edge effects. Kakamega Forest is very heterogeneous with heavy levels of disturbance even in the very centre. The plots were chosen to be representative for the respective fragmentation and disturbance regime (Bleher et al., in press, A. Althof, personal communication). The plots were dissected by five marked transects of 100 m length with neighbouring transects separated from each other by 20 m. I monitored all birds and monkeys in the early morning (0700-0830) using point counts recording all animals heard and seen within a radius of 20 m for a period of 10 minutes at nine points along the transects. Three points were placed along the first transect with each point separated from the other by 40 m, three points were placed along the third and three along the fifth transect. In the analysis, I included only bird and monkey species as frugivores which were classified either according to personal observations or being described as mainly frugivorous in the literature (Urban et al. 1986, 1997, Fry et al. 1988, 2000, Keith et al. 1992, Fry and Keith 2004). I calculated the number of species and individuals per plot and month by adding the species and individuals of the nine points per plot. For the analyses, species were categorized according to forest dependency after Bennun et al. (1996), i.e. forest specialist, forest generalist or forest visitor. Forest specialists were defined as 'true' forest birds that almost exclusively occur in undisturbed forest and invariably breed within forests (Bennun et al. 1996). Forest generalists may occur in undisturbed forests but are also common in forest strips, edges and gaps. They typically breed within the forest (Bennun et al. 1996). Forest visitors are also found within the forest but are not dependent upon it. They occur more often in non-forest habitats where they usually breed (Bennun et al. 1996).

3.2.4 Frugivore assemblage in *P. africana*

To determine the frugivore assemblage of *P. africana* I observed all fruit-eating birds and monkeys on a total of 28 randomly chosen focal trees placed on or in the vicinity of the same nine plots (as above) (Fig. 3.1). Focal trees were selected that were situated at a

distance of at least 100 m to the forest edge. The position of the 28 trees was recorded using a Global Positioning System (Garmin 12).

The observations were conducted in the months March 2002, October 2002, March 2003 and December 2003. Each of the 28 trees was observed only once during the whole study period. Observations were conducted from 0700 to 1900 in four observation blocks of three hours, each starting at the full-hour, i.e. from 0700-1000, 1000-1300, 1300-1600 and 1600-1900. The observation blocks were randomly distributed over the main fruiting period of each tree. Observations were made from an unobstructed vantage point ca. 10-20 m from the focal tree using a pair of binoculars and a stopwatch. Two methods were used to collect data:

Scan sampling: Every 30 minutes (0700, 0730, 0800, etc.) all frugivores in the focal tree were recorded for a period of one minute. Species were identified according to Zimmerman et al. (1998) and Kingdon (1997). The number of species and individuals per tree was calculated as the sum of the 25 scans corresponding to 25 minutes per day. For the analyses, species were again categorized according to forest dependency after Bennun et al. (1996), i.e. forest specialist, forest generalist or forest visitor.

Focal sampling: One individual frugivore, selected randomly, was observed from its arrival until it left the tree. The time spent in the tree, the number of fruits swallowed during its visit and its fruit handling behaviour were recorded.

In addition, for each tree I measured the diameter at breast height (dbh) and estimated the crop size by counting representative parts of the crown and then extrapolating over the whole tree crown. I estimated the crop size four times for each focal tree, i.e. in each of the four observation blocks, and calculated a mean crop size for each tree.

3.2.5 Seed dispersal of *P. africana*

To quantify the number of seeds dispersed per tree I combined scan and focal sampling data of all frugivores that swallowed the fruits. First, I calculated for each species visiting the focal tree the sum of individuals visiting the tree per 25 minutes, by adding the 25 scans. Then, I calculated for each species, using the focal sampling data, the average fruit consumption rate per minute, averaging over all focal observations of the respective species over all trees. I then multiplied for each species the number of individuals per 25 minutes with the average fruit consumption rate per minute. These products were added over all species visiting the respective tree. The resulting number gives an estimate of the number of

fruits eaten per 25 minutes per tree (25 scans x number of fruits consumed per minute). As most fruits that were eaten were dispersed away from the tree, this number gives an estimate of the number of dispersed seeds per 25 minutes per tree. Consumption rates of each species could be averaged over all trees, because I found no evidence for systematic variation in consumption rate in relation to fragmentation or disturbance regime (data not shown).

3.2.6 Fruit availability and abundance

Monitoring of the overall fruit availability of the surrounding forest was carried out in all nine study plots (see above) (Fig. 3.1) in the same months as observations were carried out, i.e. March 2002, October 2002, March 2003 and December 2003. All plants bearing ripe fruits which might be consumed by frugivorous animals were identified 10 m to the left and 10 m to the right of the five transects thereby covering a total area of 1 ha. Plant identification was carried out using Beentje (1994). For each tree the presence and number of ripe fruits were estimated *in situ* on a logarithmical scale (1 to 10, 10 to 100, 100 to 1,000, 1,000 to 10,000, > 10,000 fruits) and the number of fruits available per plot and month was calculated.

3.2.7 Statistical analysis

Regarding the analysis of the overall frugivore community I performed repeated measures ANOVA. I first tested for sphericity using Mauchly's test for sphericity (StatSoft, Inc. 2001). As sphericity was absent and as I had more repeated measures (12 months) than plots and treatment levels (9 plots, 4 treatments) I employed univariate repeated measures ANOVA (Scheiner and Gurevitch 2001, JMP 2001). In the analysis I treated fragmentation and disturbance regime and their interaction as fixed effects. Thereby, each treatment had two levels (fragmentation: main forest site or fragment; disturbance: low or high disturbance, see Fig. 3.1). The nine plots were nested within fragmentation and disturbance regime and treated as random-effects. Finally, month was included as a further fixed effect. I stepwise excluded interaction terms between month and fragmentation, and month and disturbance as they were not significant. Number of species and individuals for the overall frugivore community were log-transformed prior to analyses.

Concerning the frugivore assemblage visiting *P. africana* and the seed dispersal rate of the trees I tested the fragmentation and disturbance effect in a multivariate model using

ANOVA or ANCOVA. In the analysis I treated fragmentation and disturbance regime as fixed effects. I included also the factors crop size and fruit availability in the model. Replacing fragmentation regime by a continuous variable fragment size led to similar or less significant results. Therefore, I report only the results using fragmentation regime as a categorical variable. I stepwise excluded interaction terms, crop size and fruit availability when they were not significant. Number of species (log+1) and individuals (log+1) visiting *P. africana* trees, number of seeds dispersed per tree (log+1), crop size and fruit availability were log-transformed prior to analyses. ANOVAs and ANCOVAs were calculated using the program JMP (2001).

To test whether my data points represent statistically independent sample units, I tested for possible effects of spatial autocorrelation using an extension of the multivariate Mantel test (Smouse et al. 1986), the signed Mantel test (Oberrath and Böhning-Gaese 2001) with 20,000 permutations. These tests had to be simplified since it is not possible to perform repeated measures ANOVAs or to include interaction terms in Mantel tests. For the test of the overall frugivore community, I calculated the Euclidean distance of the mean number of frugivore species and individuals over all 12 months per study plot, of the fragmentation and disturbance regime (using dummy variables) as well as the geographical distance pairwise for all the study plots. The study plots were statistically independent when the distance in the frugivore community among the study plots did not depend on the geographical distance of the plots. Similarly, the number of frugivore species and individuals visiting *P. africana* trees, and the number of seeds dispersed per tree were tested together with the covariates crop size and fruit availability against the geographical distance of the 28 trees.

3.3 Results

3.3.1 Overall frugivore community

During the monthly census of frugivores I recorded 103 bird and four monkey species of which 49 were categorized as frugivores. I found marginally significantly fewer frugivorous species (-1.14 times) but almost similar numbers of individuals (-1.04 times) in fragments as compared to the main forest (Fig. 3.2A, B). Disturbance did not influence the frugivore community (Tab. 3.1, 3.2). The covariate month highly significantly influenced the number of species and individuals in all sites.

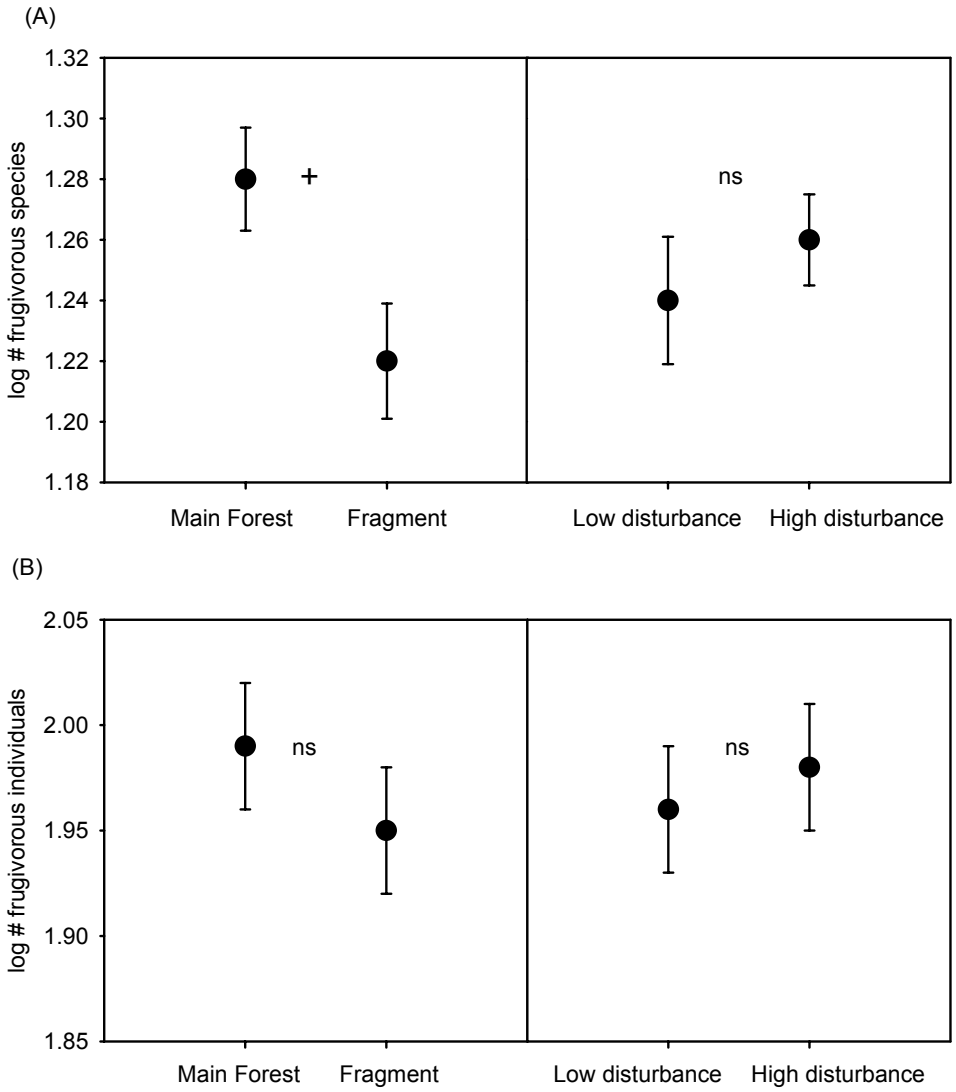


Figure 3.2: Number of frugivorous species (A) and individuals (B) in the forest in relation to fragmentation (left) and disturbance regime (right). Given are least square means (±*SE*) of univariate repeated measures ANOVA controlling for the respective other variable, month and an interaction term, ns = not significant, $^{+}$ 0.05< *P* <0.1.

Table 3.1: Number of frugivorous species (All), forest specialist species, forest generalist species and forest visitor species of the forest (all log-transformed) as a function of fragmentation, disturbance and month. Univariate repeated measures ANOVA, *N* = 108. Given are Model and Error *DF*-, *F*-, *P*-, and R^2-values; ***P<0.001, **P<0.01, $^{+}$0.05<P<0.1, ns = not significant.

	Model, Error, *DF*	All species	Forest specialists	Forest generalists	Forest visitors
Whole model	19, 88	3.84 ***	4.82 ***	4.37 ***	0.65 ns
Fragmentation	1, 5	5.44 +	2.97 ns	1.90 ns	0.54 ns
Disturbance	1, 5	0.31 ns	0.00 ns	0.03 ns	0.02 ns
Fragmentation*disturbance	1, 5	0.49 ns	0.12 ns	0.34 ns	0.20 ns
Month	11, 88	3.25 ***	2.46 **	3.93 ***	0.90 ns
R^2	-	0.44	0.50	0.47	0.12

To take into account the forest dependency of the species I repeated the analyses for species and individuals for each of the three different forest dependency categories which led to quite similar but less significant results (Tab. 3.1, 3.2). I found neither for fragmentation nor for disturbance significant effects on any of the three groups (Tab. 3.1, 3.2). Month remained the only significant covariate except for the analyses concerning the forest visitor species and individuals in which no covariate was significant (Tab. 3.1, 3.2).

Table 3.2. Number of frugivorous individuals (All), forest specialist individuals, forest generalist individuals and forest visitor individuals of the forest (all log-transformed) as a function of fragmentation, disturbance and month. Univariate repeated measures ANOVA, N = 108. Given are Model and Error DF-, F-, P-, and R^2-values; ***P<0.001, **P<0.01, ns = not significant.

	Model, Error, *DF*	All individuals	Forest specialists	Forest generalists	Forest visitors
Whole model	19, 88	5.84 ***	3.43 ***	7.58 ***	0.80 ns
Fragmentation	1, 5	0.96 ns	0.41 ns	1.99 ns	0.06 ns
Disturbance	1, 5	0.13 ns	0.10 ns	0.14 ns	0.02 ns
Fragmentation*disturbance	1, 5	0.06 ns	0.27 ns	0.33 ns	0.07 ns
Month	11, 88	7.64 ***	2.87 **	9.88 ***	1.12 ns
R^2	-	0.54	0.41	0.61	0.14

The number of frugivore species and individuals per plot did not depend on the geographical distance among the plots (Multivariate Signed Mantel test: effect of geographical distance: $t < 0.87$, $P > 0.33$, respectively; pairs of plots = 36).

3.3.2 Frugivore assemblage in *P. africana*

During 336 h of tree observations, I recorded 75 bird and three monkey species visiting the *P. africana* trees of which 36 were categorized as frugivores (Tab. 3.3). The most frequent frugivores were Common Bulbul (348 individuals), Violet-backed Starling (131), Yellow-whiskered Greenbul (108), Blue Monkey (94), Blackcap (83) and Red-tailed Monkey (79) (Tab. 3.3). I recorded highly significantly (1.47 times) more frugivorous species and significantly (1.61 times) more individuals in highly disturbed than in less disturbed sites (Tab. 3.4, 3.5, Fig. 3.3, 3.4). Effects of fragmentation on numbers of species and individuals were not significant but a tendency for higher numbers of species (1.13 times) and individuals (1.24 times) in fragments was apparent (Fig. 3.3, 3.4). I found a marginally

significant negative effect of crop size and no effect of fruit availability on species as well as individuals (Tab. 3.4, 3.5). Moreover, the analyses revealed a highly significant interaction between fragmentation and crop size (increase of species and individuals with increasing crop size in main forest sites, decrease of species and individuals with increasing crop size in fragments) and a significant interaction between disturbance and fruit availability (increase of species and individuals with increasing fruit availability in little disturbed sites, steeper increase of species and individuals with increasing fruit availability in highly disturbed sites) (Tab 3.4, 3.5).

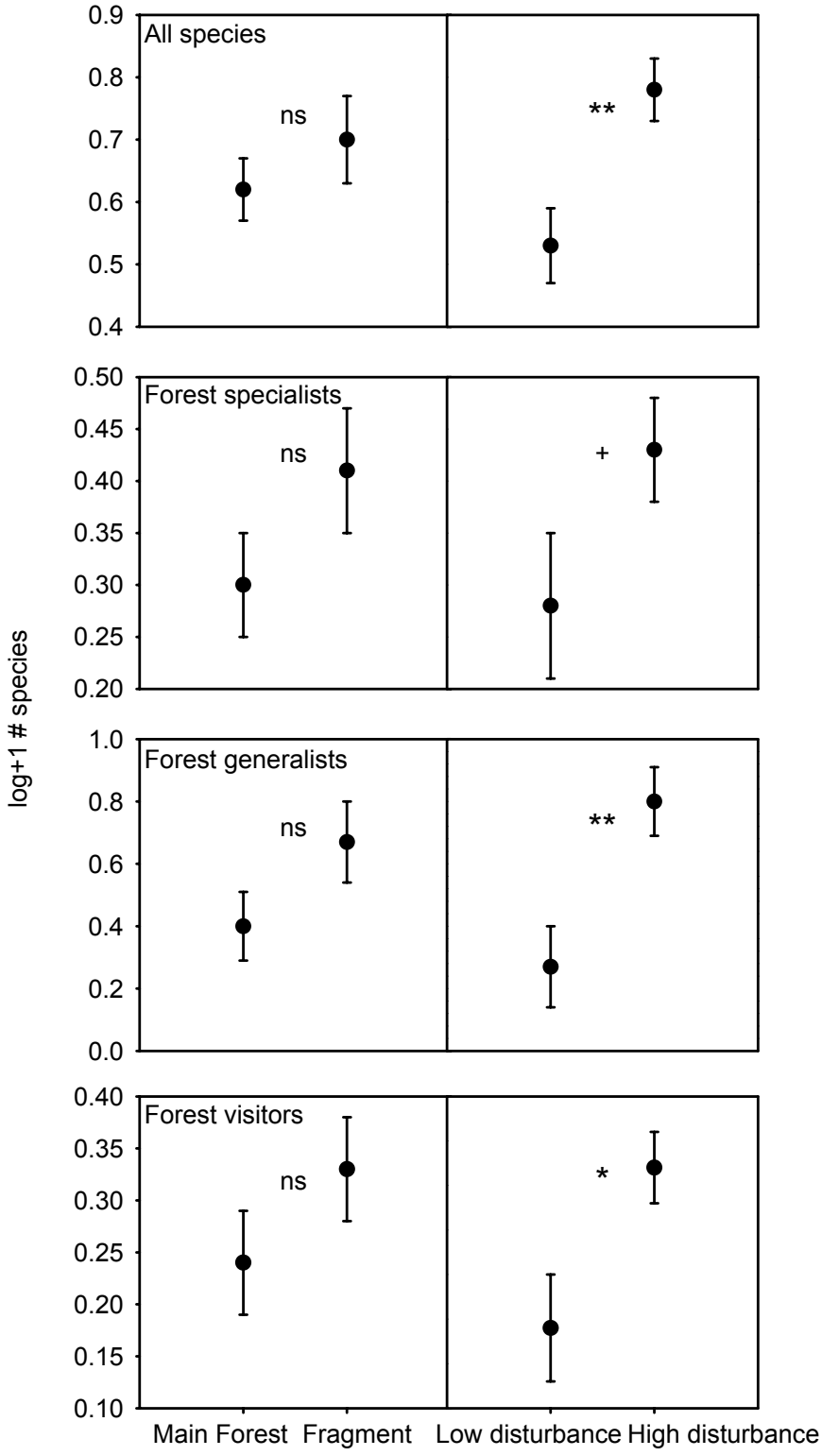


Figure 3.3: Number of all frugivorous species, forest specialist species, forest generalist species and forest visitor species in *P. africana* trees recorded during 25 scan samples in relation to fragmentation (left) and disturbance regime (right). Given are least square means (±*SE*) controlling for the respective other covariates as well as for crop size, fruit availability and potential interaction terms, ns = not significant, $^{+}$ 0.05< *P* <0.1, **P* <0.05, ***P* <0.01.

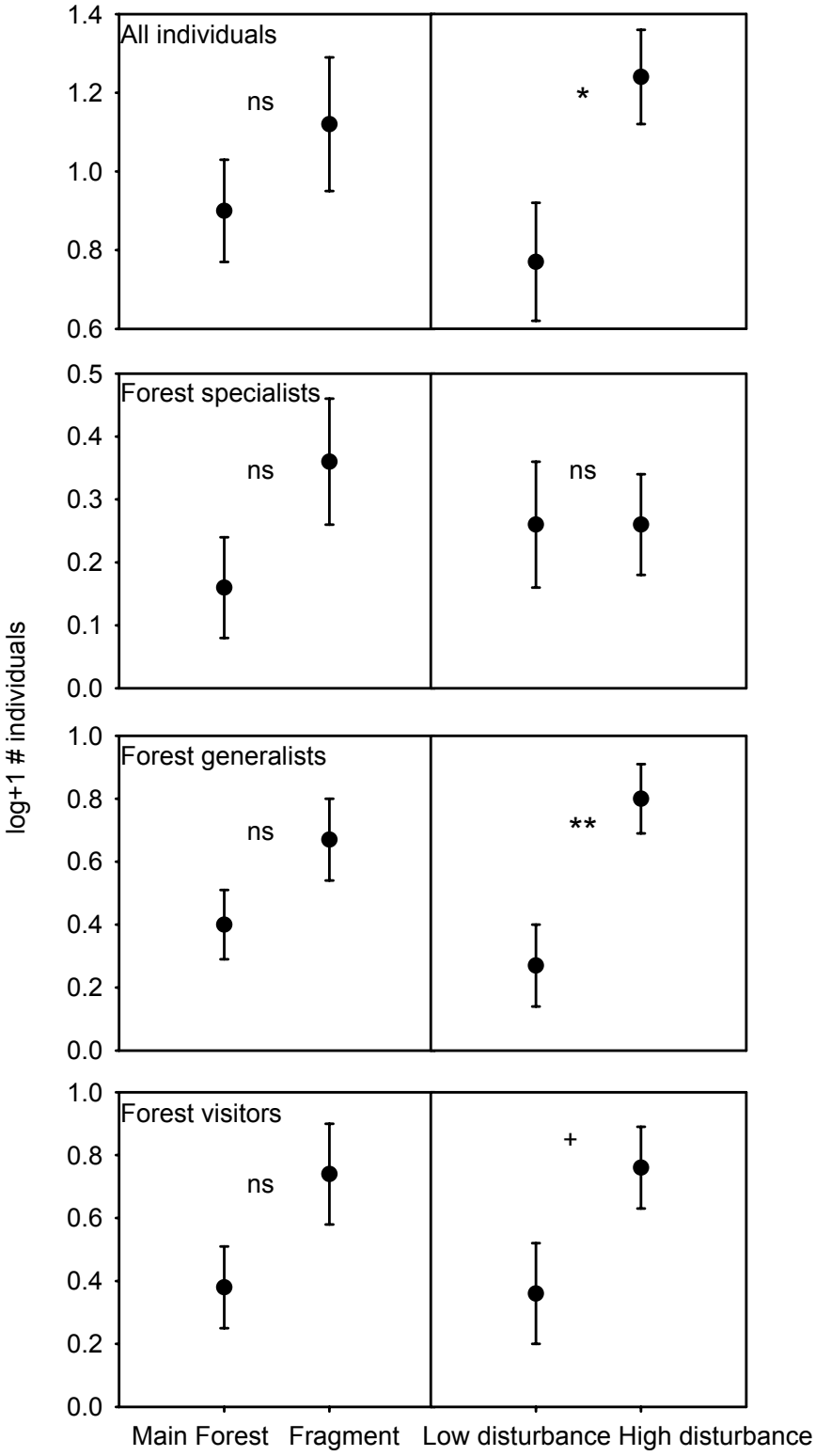


Figure 3.4: Number of all frugivorous individuals, forest specialist individuals, forest generalist individuals and forest visitor individuals in *P. africana* trees recorded during 25 scan samples in relation to fragmentation (left) and disturbance regime (right). Given are least square means (±*SE*) controlling for the respective other covariates as well as for crop size, fruit availability and potential interaction terms, ns = not significant, $^{+}$ 0.05< *P* <0.1, **P* <0.05, ** <0.01.

Table 3.3: List of the 36 frugivore species visiting *P. africana* trees with their fruit handling-behaviour, number of fruits swallowed per minute , sum of individuals observed during the 25 scan samples over all 28 trees, dependency on forest, body-size and their presence during scan sampling in main forest, fragmented, low and high disturbed sites, respectively.

Vernacular Name *Scientific Name*	Fruit handling-behaviour[1]	Fruits* min^{-1}	∑ of individuals over all 28 trees[2]	Forest depen-dency[3]	Body-size[4] (cm)	Main Forest	Fragment	Low disturbance	High disturbance
African Thrush *Turdus pelios*	s	1.27	8	FV	22.0	+	-	+	-
Baglafecht Weaver *Ploceus baglafecht*	p	0	*	FV	15.0	-	-	-	-
Black & white-casqued Hornbill *Bycanistes subcylindricus*	s	2.78	23	FG	78.0	-	+	-	+
Black & white Colobus Monkey *Colobus guereza*	s, d, c	3.71	66	FG	60.5	+	+	+	+
Blackcap *Sylvia atricapilla*	p, s	0.35	83	FG	14.0	+	+	+	+
Blue Monkey *Cercopithecus mitis*	s, d, c	2.18	94	FS	53.3	+	+	-	+
Brown-capped Weaver *Ploceus insignis*	p, s	0.18	2	FS	12.7	-	+	+	+
Cabanis Greenbul *Phyllastephus cabanisi*	p, s	0.44	7	FS	18.0	+	-	-	+
Cameroon Sombre Greenbul *Andropadus curvirostris*	s	0.66	1	FS	16.5	-	-	-	+
Common Bulbul *Pycnonotus barbatus*	s	0.86	348	FV	20.0	+	+	+	+
Double-toothed Barbet *Lybius bidentatus*	s	0.61	1	FV	23.0	-	-	-	-
Garden Warbler *Sylvia borin*	p, s	0.54	31	FV	14.5	-	+	-	+
Grey-throated Barbet *Gymnobucco bonapartei*	p, s	0.66	42	FG	20.0	+	+	-	+
Hairy-breasted Barbet *Tricholaema hirsuta*	s	1.48	*	FG	16.5	-	-	-	-
Honeyguide Greenbu *Baeopogon indicator*	s	0.63	2	FS	20.0	+	+	-	+
Joyful Greenbul *Chlorocichla leatissima*	s	0.96	27	FG	20.0	+	+	+	+
Little Greenbul *Andropadus virens*	s	0.80	*	FG	15.5	+	+	-	+
Little Grey Greenbul *Andropadus gracilis*	p, s	0.25	10	FS	15.0	-	-	-	-
Olivaceous Warbler *Hippolais pallida*	p, s	0.18	35		13.0	-	+	+	+
Olive Thrush *Turdus olivaceus*	p, s	0.95	33	FG	24.0	+	+	-	+
Red-tailed Monkey *Cercopithecus ascanius*	s, d, c	1.64	79	FS	45.5	+	+	+	+
Shelley's Greenbul *Andropadus masukuensis*	s	0.64	6	FS	16.5	-	+	-	+

Vernacular Name *Scientific Name*	Fruit handling-behaviour[1]	Fruits* min^{-1}	∑ of individuals over all 28 trees[2]	Forest depen-dency[3]	Body-size[4] (cm)	Main Forest	Fragment	Low disturbance	High disturbance
Slender-billed Greenbul *Andropadus gracilirostris*	p, s	0.65	18	FS	17.5	+	+	-	+
Spectacled Weaver *Ploceus ocularis*	p	0	2	FV	15.5	-	+	+	-
Stuhlmanns Starling *Poeoptera stuhlmanni*	s	0.28	7	FS	15.0	-	+	-	+
Tambourine Dove *Turtur tympanistria*	p	0	1	FG	22.0	-	+	-	+
Toro Olive Greenbul *Phyllastrephus hypochloris*	p	0	1	FS	18.0	-	+	+	+
Ugandan Woodland Warbler *Phylloscopus trochilus*	p	0	2	FS	11.5	-	+	-	+
Violet-backed Starling *Cinnyricinclus leucogaster*	p, s	0.46	131	FV	18.2	-	+	-	+
Willow Warbler *Phylloscopus sibilatrix*	p	0.03	17	FV	12.5	+	+	+	+
Yellow-billed Barbet *Trachylaemus purpuratus*	p, s	0.82	2	FG	25.0	+	-	-	+
Yellow-rumped Tinkerbird *Pogoniulus subsulphureus*	s	0.42	2	FS	10.0	+	-	-	+
Yellow-spotted Barbet *Buccanodon duchaillui*	p, s	0.47	3	FS	15.0	-	+	-	+
Yellow Throated Leaflove *Chlorocichla flavicollis*	s	1.22	3	FV	20.0	+	+	-	+
Yellow-whiskered Greenbul *Andropadus latirostris*	p, s	1.03	108	FG	17.2	+	+	-	-
Yellow White Eye *Zosterops senegalensis*	p	0	26	FV	11.5	-	+	+	+

[1]Fruit handling-behaviour: p = peck on fruits, s = swallow fruits, d = drop seeds, c = crush seeds.
[2]∑ individuals over all 28 trees: * = no data as species has only been observed during focal sampling and not during scan sampling.
[3]Forest dependency: FS = forest specialist, FG = forest generalist, FV = forest visitor after Bennun et al. (1996), for monkeys (M. Cords, C. Chapman, personal communication).
[4]Body-size of monkeys (head to bottom) after Kingdon (1997) and of birds (tip of beak to tip of tail) after Urban et al. (1986, 1997), Fry et al. (1988, 2000), Keith et al. (1992), Fry and Keith (2004).

To take into account the degree of forest dependency of species I repeated the analyses for species and individuals for each of the three different forest dependency categories leading to quite similar results (Tab. 3.4, 3.5, Fig. 3.3, 3.4). The analyses revealed a marginally significant positive effect of disturbance on forest specialist species and a significant positive effect of fruit availability and a significant interaction between fragmentation and crop size (pattern as above) for forest specialist individuals (Tab. 3.4, 3.5). Regarding forest generalist species and individuals I found in both analyses

a highly significant positive effect of disturbance, a significant negative effect of crop size and a highly significant interaction between fragmentation and crop size (pattern as above) (Tab. 3.4, 3.5). The analyses for forest visitor species revealed a significant positive effect of disturbance and a marginally significant positive effect of fruit availability, and for forest visitor individuals a marginally significant positive effect of disturbance and negative of crop size, a significant positive effect of fruit availability and a highly significant interaction between fragmentation and crop size (pattern as above) (Tab. 3.4, 3.5).

Table 3.4. Number of frugivorous species (All), forest specialist species, forest generalist species and forest visitor species (log+1-transformed) of *P. africana* as a function of fragmentation, disturbance, log crop size and log fruit availability. ANCOVA type III SS, $N = 28$. Given are Model and Error *DF*-, *F*-, *P*-, and R^2-values; ***$P<0.001$, **$P<0.01$, *$P<0.05$, $^{+}0.05<P<0.1$, ns = not significant.

	All species	Forest specialist	Forest generalists	Forest visitors
Model, Error *DF*	6, 21	2, 25	4, 23	3, 24
Whole Model	7.72 ***	3.38 +	9.09 ***	5.20 **
Fragmentation	0.80 ns	1.57 ns	2.38 ns	1.59 ns
Disturbance	8.93 **	3.17 +	9.82 **	5.69 *
Log crop size	3.03 +	-	5.11 *	-
Log fruit availability	2.09 ns	-	-	4.25 +
Fragmentation* log crop size	10.67 **	-	8.92 **	-
Disturbance* log fruit availability	6.96 *	-	-	-
R^2	0.69	0.21	0.61	0.39

The number of frugivorous species and individuals per tree did not depend on the geographical distance among the trees (Multivariate Signed Mantel Test: effect of geographical distance: $t < 2.24$, $P > 0.14$, respectively; pairs of trees = 378).

The 36 frugivorous species were not all present in the different fragmentation and disturbance regimes (Tab. 3.3). Higher numbers of individuals on trees in fragmented and disturbed sites were observed in 28 out of the 36 frugivores species. Only two species, African Thrush and Double-toothed Barbet, were more abundant in main forest and in less disturbed sites. However, small numbers of individuals prevented rigorous statistical analyses of individual species.

Table 3.5. Number of frugivorous individuals (All), forest specialist individuals, forest generalist individuals and forest visitor individuals (log+1-transformed) of *P. africana* as a function of fragmentation, disturbance, crop size and fruit availability. ANCOVA type III SS, $N = 28$. Given are Model and Error *DF*-, *F*-, *P*-, and R^2-values; ***P<0.001, **P<0.01, *P<0.05, $^{+}$0.05<P<0.1, ns = not significant.

	All individuals	Forest specialist	Forest generalist	Forest visitors
Model, Error DF	6, 21	5, 22	4, 23	5, 22
Whole Model	6.13 ***	3.15 *	9.09 ***	6.24 **
Fragmentation	0.92 ns	2.25 ns	2.38 ns	2.77 ns
Disturbance	5.43 *	< 0.01 ns	9.82 **	3.60 +
Log crop size	4.31 +	0.03 ns	5.11 *	3.99 +
Log fruit availability	1.44 ns	6.94 *	-	5.08 *
Fragmentation* log crop size	10.15 **	6.41 *	8.92 **	9.09 **
Disturbance* log fruit availability	4.57 *	-	-	-
R^2	0.64	0.42	0.61	0.59

3.3.3 Seed dispersal of *P. africana*

With regard to seed dispersal I found 1.51 times more seeds dispersed per tree in fragments compared to main forest and 1.48 times more seeds dispersed per tree in more disturbed sites than in less disturbed sites, both marginally significant (ANOVA type III SS, log+1 # seeds per tree: whole model, $R^2 = 0.31$, $F_{2,25} = 5.76$, $P = 0.0088$; fragmentation: $F_{1,25} = 4.21$, $P = 0.051$, disturbance: $F_{1,25} = 3.74$, $P = 0.064$, Fig. 3.5).

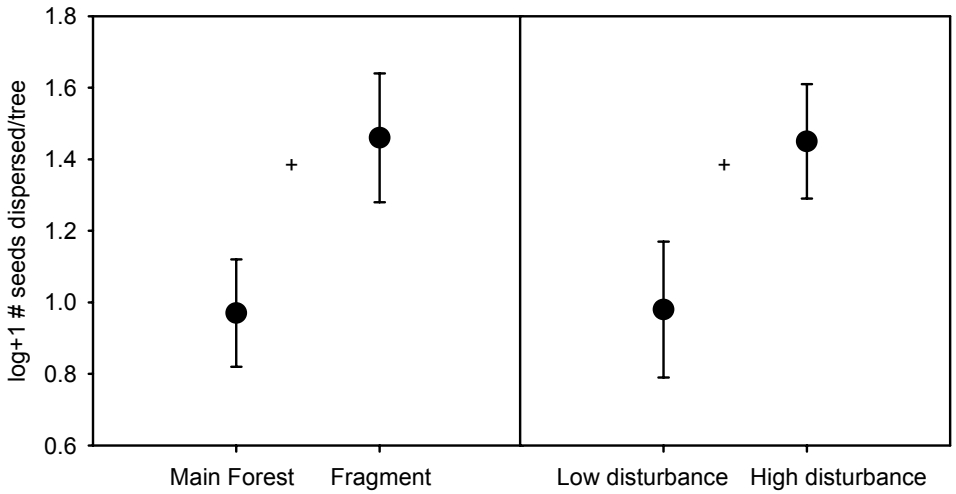


Figure 3.5: Numbers of seeds dispersed per tree in 25 min. in relation to fragmentation (left) and disturbance regime (right). Given are least square means (±*SE*); $^{+}$ 0.05< P <0.1.

The test controlling for spatial autocorrelation between the 28 trees revealed that seed dispersal did not depend on the geographical distance among the trees (Multivariate Signed Mantel test: effect of geographical distance: $t = 1.24$, $P = 0.30$, pairs of trees = 378).

3.4 Discussion

3.4.1 Overall frugivore community

My results on the overall frugivore community demonstrated a trend towards declining frugivores due to fragmentation with marginally significantly fewer species in fragmented sites. These results correspond to a number of other studies that showed declines of frugivores due to forest fragmentation (Guitian et al. 1992, Cordeiro and Howe 2003, Luck and Daily 2003). I found a marginally significant fragmentation effect but no disturbance effect on the overall frugivore community. A reason for this pattern could be that disturbance changes the habitat on a smaller spatial scale than fragmentation. In general, frugivores are quite mobile species with big territories ranging across open landscapes (Sun 1997, Restrepo and Gomez 1998, Westcott and Graham 2000). Thus, frugivores might be less responsive to disturbance or even increase in abundance in disturbed areas due to compensatory effects of generalists and forest-edge species (Dranzoa 1998). In my study, the three forest dependency groups were not significantly affected by disturbance but all showed similar tendencies. Thus, in my study compensatory effects of forest generalists or forest visitors replacing forest specialists in the frugivore community were not apparent. Fragmentation acts across larger spatial scales and distances among different fragments or fragments and the main forest might not be readily crossed even by frugivores. Again, the three forest dependency groups were affected similarly with no indication to forest specialists being differently affected than forest generalists or visitors.

3.4.2 Frugivore assemblage and seed dispersal in *P. africana*

In contrast to the overall frugivore community, *P. africana* trees were visited by higher numbers of dispersal agents (species and individuals) in disturbed sites and had marginally significantly higher seed dispersal rates in fragments and in disturbed sites. My data contrast to results of Cordeiro and Howe (2003) who found a decline of avian species visiting *Leptonychia usambarensis* in fragments (2-31 ha). Similarly, Santos and Tellería (1994) showed a lower abundance of thrushes (*Turdus* spp.) visiting *Juniperus* trees in

small forest fragments (0.2-16 ha). In a 250 ha fragment of old-secondary forest Pizo (1997) recorded only 14 out of 35 bird species from the continuous Atlantic rain forest feeding on *Cabralea canajerana*. My contrary results could be explained with the larger sizes of the fragments in my study (130-1,400 ha) as compared to the others. Apart from the study of Pizo (1997) the largest fragments in the two studies of Cordeiro and Howe (2003) and Santos and Tellería (1994) are much smaller than the smallest in my study. If fragments adjacent to Kakamega Forest continue to decrease in size (Fig. 3.1) the observed decline of the frugivore species richness in fragments might lead to a depauperate frugivore assemblage on *P. africana* in the long-term as well.

The results indicate a tendency towards more frugivores on *P. africana* trees and marginally significantly more seed dispersal in fragments than in main forest sites although fragments have a somewhat impoverished frugivore community. Moreover, I recorded significantly more frugivores and marginally significantly more seed dispersal in highly disturbed sites in spite of no significant difference in the frugivore community. Obviously, *P. africana* trees are disproportionately attracting frugivores especially in more disturbed sites. One possible reason for higher numbers of frugivores in *P. africana* trees situated in more disturbed sites could be higher crop sizes and higher overall fruit availability in these sites. Large crop size and large overall fruit availability often attract many birds (Santos and Tellería 1994, Rey 1995, Levey and Benkman 1999, Garcia and Ortiz-Pulido 2004). However, in my statistical analysis I controlled for the potentially confounding effects of crop size and fruit availability. Thus, neither the fruit supply of individual *P. africana* trees nor the general fruit availability alone was responsible for causing the differences among sites. Alternatively, the general food supply could be impoverished in fragments and highly disturbed sites leading to a special attractiveness of fruiting trees. This would explain the accumulation of frugivores in the remaining fruiting trees. These assumptions suggest that fruiting trees such as *P. africana* are an important resource for frugivorous birds potentially providing longer survival of frugivores in fragments and disturbed sites as demonstrated in other studies (Luck and Daily 2003, Murphy and Lovett-Doust 2004).

In the analyses concerning the three forest dependency groups I revealed similar responses of the three groups to fragmentation and disturbance regime. Thus, not only forest visitors or generalists but also forest specialists contributed to the increase in visitation rate and seed dispersal of *P. africana* trees especially in disturbed sites. It has been argued that different groups of forest birds show compensatory responses to

disturbance and fragmentation with a corresponding stability of their total ecosystem service (Brotons et al. 2003). However, I found no indication that forest visitors or generalists showed compensatory responses to forest specialists. In studies on pollination affected by habitat fragmentation and disturbance, the decline in visits by native species was compensated by an alien pollinator (Aizen and Feinsinger 1994, Dick 2001). In contrast, in my study, all forest dependency groups as well as most of the species increased in abundance in *P. africana* trees in fragments and disturbed sites. In general, plant species with potentially interchangeable pollinators or seed dispersers might be less sensitive to fragmentation or disturbance (Aizen and Feinsinger 1994). However, redundancy of species that compensate ecosystem services might exist only up to a certain degree and the functioning of processes may also depend on some species more than on others. Therefore, loss of species diversity can be a problem in the long-term as redundant species might act as ecosystem buffers against future environmental change (Loreau et al. 2001).

The marginally significant increase in the number of seeds removed from *P. africana* trees in fragmented and heavily disturbed sites indicates that the important process of seed dispersal in the life cycle of *P. africana* seems to be slightly strengthened in these sites in Kakamega Forest. Many studies have shown that seed dispersal away from the parent tree through avian frugivores is important for tree regeneration (Bleher and Böhning-Gaese 2001, Wenny 2001, Luck and Daily 2003, Makana and Thomas 2004) and for maintaining genetic variation (Loveless and Hamrick 1984, Ledig 1986). The results of the present study demonstrate that when studying the consequences of fragmentation and disturbance, it is important to consider both, species composition as indicator for biodiversity on the one side, and processes such as seed dispersal as indicator for the function of ecosystems on the other side, because they might respond in opposite directions (Herrera 2000, Steffan-Dewenter et al. 2001, Balcomb and Chapman 2003, Andresen and Levey 2004).

However, when interpreting the results of my study, one has to keep in mind that I was able to quantify only the number of seeds that were dispersed away from the parent tree and not the quality of seed dispersal. The quality of seed dispersal depends on the one side on the quality of treatment given a seed in the mouth and in the gut and on the other side on the quality of seed deposition as determined by the probability that a deposited seed will survive and become an adult (Schupp 1993). Moreover, seed dispersal is only one process in the life cycle of trees. Other processes such as seed predation or seedling

herbivory might be higher in fragmented and disturbed sites (Santos and Tellería 1994, Asquith et al. 1997, Debinski and Holt 2000, Donoso et al. 2004). A trend towards increased seed dispersal does not necessarily imply that the tree species regenerates sufficiently and maintain sustainable populations (Daily et al. 2001). In fact, *P. africana* populations in the south of Kakamega Forest show rapid declines (Fashing 2004). Thus, while the quantity of seed dispersal seems to be slightly enhanced in fragments and highly disturbed sites, other processes in the life cycle of the tree might be negatively affected by fragmentation and disturbance and cause diminished establishment and declines in the tree population. Thus, in the future, all processes of the life cycle must be taken into account to evaluate the effects of fragmentation and disturbance on the regeneration potential and population size of *P. africana* in Kakamega Forest.

3.5 Summary

Forest destruction and disturbance can have long-term consequences for species diversity and ecosystem processes such as seed dispersal. Understanding these consequences is a crucial component of conserving vulnerable ecosystems. In the heavily fragmented and disturbed Kakamega Forest, western Kenya, I studied seed dispersal of *Prunus africana* (Rosaceae). In the main forest, five forest fragments, and differently disturbed sites I quantified the overall frugivore community as an indicator for species diversity. Furthermore, I determined the frugivores on 28 fruiting *P. africana* trees, estimated seed dispersal, crop size and the general fruit availability of surrounding trees. During the overall frugivore census I recorded 49 frugivorous species; 36 of them were observed visiting *P. africana* trees and feeding on their fruits. Although overall frugivore species richness was 1.1 times lower in fragments than in main forest sites and 1.02 times higher in highly disturbed than in less disturbed sites, *P. africana* experienced 1.1 times higher numbers of frugivores in fragments than in main forest sites and 1.5 times higher numbers of frugivores in highly disturbed than in less disturbed sites. Correspondingly, seed dispersal was 1.5 times higher in fragments than in main forest sites and 1.5 times higher in more disturbed than less disturbed sites. Fruit availability of surrounding trees and crop size influenced the number of visitors to some degree. Thus, the number of dispersed seeds seemed to be slightly higher in fragmented and highly disturbed sites. This indicates that there is a certain degree of redundancy in an ecosystem which may compensate loss of single species.

However, loss of diversity could be a problem in the long-term as redundant species might act as buffers against future environmental change.

4 CONSEQUENCES OF FRAGMENTATION AND DISTURBANCE FOR SEED PREDATION

4.1 Introduction

The last decades have seen a general biodiversity decline especially in tropical forests, with the major threats being deforestation, forest fragmentation and disturbance (Turner and Corlett 1996, Whitmore 1997, Laurance, et al. 2000). Populations of plants and animals respond to these human induced changes in variable ways ranging from declines to increases. The responses depend on the species' characteristics and the particular level of fragmentation and disturbance involved (Kruess and Tscharntke 1994, Santos and Tellería 1994, Cole et al. 1995). Long-term consequences for ecosystem processes are expected (Chapin et al. 2000). Despite their importance for conservation, these processes are hardly understood (Didham et al. 1996).

Forest fragmentation and disturbance can influence the life cycle of a plant species at different levels. For example, fragmentation can lead to a decline in pollinator abundance and diversity leading to a decrease in pollination success and seed set of wild plant species (Cunningham 2000). Fragmentation has also been shown to lead to a decline of avian seed dispersers, a decrease in dispersal of seeds from a tropical bird-dispersed tree and a decline of seedlings occurring > 10 m from parent trees (Cordeiro and Howe 2003). Furthermore, fragmentation and disturbance have been demonstrated to modify abundance and distribution of rodents and in turn seed predation (Terborgh and Wrigth 1994, Asquith et al. 1997, Harrington et al. 1997). Some studies showed that in small fragments and at forest edges the abundance of rodents increased compared to large fragments and the forest

interior (Sork 1987, Santos and Tellería 1994, Asquith et al. 1997, Donoso et al. 2004), whereas others found that abundance and diversity of rodents decreased due to fragmentation (Turner and Corlett 1996, Harrington et al. 1997). These changes in the different processes may influence seed mortality and in turn alter tree recruitment. Although these studies demonstrated that fragmentation and disturbance can have severe effects on pollination, seed dispersal and seed predation it is not clear which of these processes is most affected. In addition, fragmentation and disturbance seem to have positive or negative consequences for the processes in the life cycle of a plant. One reason for this lack of understanding is that hardly more than one process has been studied in the same species (but see Santos and Tellería 1994 on seed dispersal and predation in *Juniperus thurifera*).

In a previous study I investigated the influence of forest fragmentation and disturbance on seed dispersal in the endangered Afrotropical tree *Prunus africana* in Kakamega Forest, western Kenya (see chapter 3). Its populations have been declining in many forests due to unsustainable exploitation of bark for the international medicinal plant trade (Cunningham and Mbenkum 1993). Surprisingly, fragmentation and disturbance appeared to lead to an increase of frugivore numbers and seed dispersal rather than a decrease in fragmented and highly disturbed sites compared to main forest and less disturbed sites. In a next step I wanted to understand, whether the recorded change in seed dispersal of the species is similar in seed predation or whether the increase in seed dispersal is possibly compensated by an increase in seed predation.

The objective of my study was to understand the consequences of fragmentation and disturbance on seed predators and seed predation rates of *P. africana*. Since the seed predation rate is influenced by small mammals, I first tested whether fragmentation and disturbance have consequences for the activity of small mammals. Second, I performed feeding experiments to identify potential seed predators. Third, I determined whether fragmentation and disturbance affect the predation rate of *P. africana* seeds. Finally, I related seed predator activity to predation rates.

4.2 Material and Methods

4.2.1 Study area

The study took place in Kakamega Forest, western Kenya (between latitudes 0°14' and 0°21'N and longitudes 34°47' and 34°48'E). Kakamega Forest is the eastern most relict of the Guineo-Congolian rainforest belt and lies at an altitude of 1,500 to 1,700 m asl. (Kokwaro 1988). Average annual temperature in the forest is between 10.6° and 27.7°C (Tsingalia 1990); annual precipitation averages 2,007 mm and is highly seasonal with a rainy season from April to November and a short dry season from December to March (as averaged from Forest Department records at Isecheno Forest Station from 1982 to 2001). The forest covers an area of 8,500 ha of a main forest block surrounded by five forest fragments of various sizes (130–1400 ha), Malava and Kisere in the north, and Yala, Ikuywa and Kaimosi in the south (Fig. 4.1A). I treat Yala and Ikuywa as two different fragments because they are separated by a road that cuts through a very narrow corridor of trees still connecting the two fragments. The northern part of the main forest block and the fragment Kisere are managed by the Kenya Wildlife Service (KWS) showing lower levels of human disturbance such as lower numbers of logged trees. The southern part of the main forest block and the fragments Yala, Ikuywa, Malava and Kaimosi are managed by the Forest Department (FD) and are characterized by higher levels of disturbance connected with high numbers of logged trees (Bleher et al., in press). The forest is surrounded by a densely settled area (600 people/km^2) (KIFCON 1994). Further information on the fragmentation and disturbance history of Kakamega Forest is given in Tsingalia (1990) and Mitchell (2004).

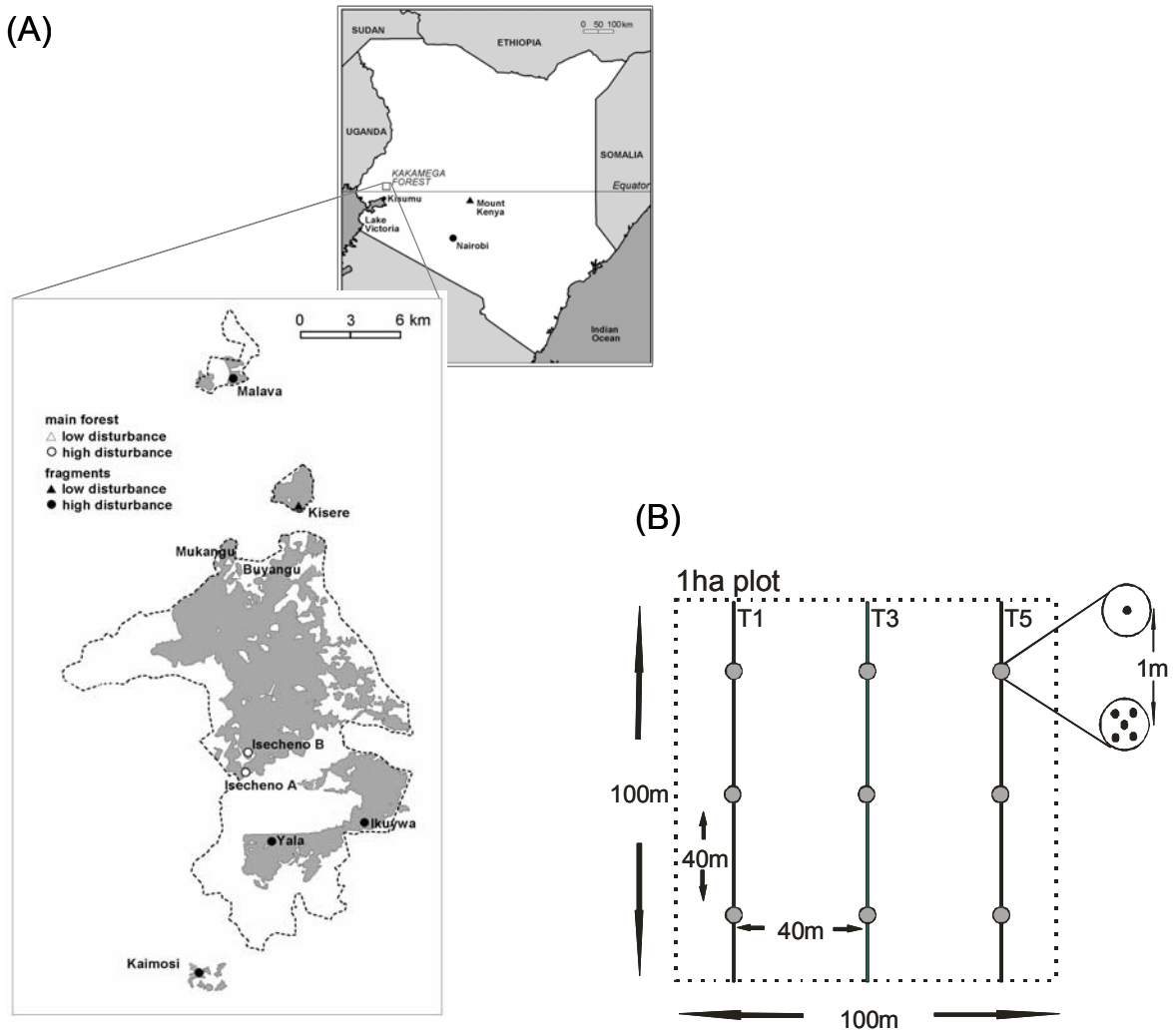


Figure 4.1A: Map of Kenya indicating location of Kakamega Forest and detailed map of Kakamega Forest: Main forest and adjacent fragments with location of the nine study plots. Dashed line represents former forest boundary (1933), grey shading represents actual forest cover. Courtesy of G. Schaab. **B**: Research design for assessing predation rates of *P. africana* seeds. Shown are the 9 positions of the dish pairs on transect 1, 3 and 5 in the 1-ha plot.

4.2.2 Study species

Prunus africana Hook f. (Rosaceae) is an evergreen tree species native to Africa and Madagascar typical of mature climax forests. The monoecious tree grows up to 40 m in height and has small white flowers in elongated clusters which are basically insect-pollinated (personal observations). It has purple fleshy one-seeded fruits (seeds: diameter: 6.6 ± 0.5 mm, mass: 0.15 ± 0.05 g, $N = 30$) which are dispersed by birds and monkeys (see chapter 3).

4.2.3 Seed predator activity

To test the influence of fragmentation and disturbance on the activity of small mammals I trapped small mammals on the forest floor in the dry season from 24.01.-22.02.2003 and in the rainy season from 26.04.-22.05.2003. I set up Sherman live-traps (9.84 x 11.47 x 29.52 cm) in nine 1-ha plots, four sites in the main forest block, i.e. Mukangu, Buyangu, Isecheno A and Isecheno B, and five in fragments with one in each of the five fragments Malava, Kisere, Ikuywa, Yala and Kaimosi (Fig. 4.1A). All plots were placed at a distance of at least 100 m to the forest edge to avoid edge-effects. Kakamega Forest is very heterogeneous with heavy levels of disturbance even in the very centre. The plots were chosen to be representative for the respective fragmentation and disturbance regime (Bleher et al., in press, A. Althof, personal communication). In each plot, traps were set up along five marked and four unmarked transects of 100 m length with neighbouring transects separated from each other by 10 m. Along each of the nine transects I set up eleven Sherman live-traps on the ground with a distance of 10 m between traps starting from 0 m (total 99 traps per plot). During both, the dry and rainy season, trapping in one plot was conducted for three consecutive nights. I used peanut butter as bait as it is known to attract a high variety of small mammal species. Traps were set before dusk and collected the next morning. Caught animals were identified using Kingdon (1997). Since I did not mark animals before release, I could not determine whether the same individual was re-captured in the three nights and in the two seasons. Therefore, my measure of abundance does not reflect the number of individuals but the activity of individuals. For each trapping season I calculated the mean number of small mammals caught per night and plot over the three trapping nights per plot. Thus, my measure of predator activity is the mean number of individuals caught per night and plot pooled for the three trapping nights.

To confirm whether small mammals caught in Sherman traps act as possible seed predators of *P. africana* I kept the different species separately in cages and offered ten *P. africana* seeds for a period of 24 h. The animals were released the next morning at the same position where caught and I looked for remaining *P. africana* seeds or husks in the cages to identify whether or not the species preyed upon these seeds. Similar feeding experiments were conducted in February and March 2004 (M. Melcher, unpublished data).

4.2.4 Predation rates

To assess the predation rates on *P. africana* seeds I arranged two plastic dishes (0.5 cm depth, 12 cm diameter) in pairs separated by 1 m at nine positions on the nine 1-ha plots (see above) following the trapping sessions, i.e. from 19.03.-02.04.2003 (dry season) and from 15.05.-30.05.2003 (rainy season). Three dish pairs were placed along the first marked transect with each pair separated from the other by 40 m, three dish pairs were placed along the third and three along the fifth transect (Fig. 4.1B). One of the two dishes was baited with one seed and the other one with five *P. africana* seeds. These experiments were performed for two consecutive nights. I replaced seeds that disappeared during the first night and that of which just seed remnants remained on or around the dish for the second night. Since I could not distinguish whether seeds that disappeared were dispersed or preyed upon, I classified only the seeds of which remnants, i.e. husks of seeds, remained on or close to the dishes as definitely preyed upon. I calculated the mean percentage of seeds preyed upon per dish and plot over the two nights, separately for 1-seed dishes and 5-seeds dishes and for each season. Thus, my measure of seed predation is, again, the proportion of seeds preyed upon per night and plot pooled for the two nights. Percentages were arcsine square root transformed prior to statistical analysis (Sokal and Rohlf, 1995).

To see whether the predation risk for seeds is density-dependent, i.e. higher for the 5-seeds dishes than for the 1-seed dishes, I compared the percentage of seeds preyed upon between the 1-seed dishes and the 5-seeds dishes. To test for effects of fragmentation and disturbance I analysed the difference in the percentage of preyed upon seeds between 1-seed and 5-seeds dishes, i.e. the degree of density dependence, as a function of fragmentation and disturbance regime.

To relate seed predator activity to predation rates I correlated the activity of seed predators with the percentage of seeds preyed upon for 1-seed and for 5-seeds dishes.

4.2.5 Statistical analyses

I treated the nine study plots as statistically independent sampling units because the closest distance between any two plots was 1,100 m which is much beyond the size of the home range of any of the species studied. I tested the fragmentation and disturbance effect in a multivariate model using ANOVA after verifying that data and residuals were normally distributed. Thereby, fragmentation and disturbance were treated as nominal variables,

comparing the plots in main forest against fragments and the plots under high against low disturbance regime. I excluded the interaction term between fragmentation and disturbance when it was not significant. Replacing the nominal variable fragmentation by the size of the main forest and fragments, respectively, led to very similar results. I used the program JMP (2001) for all statistical analyses.

4.3 Results

4.3.1 Seed predator activity

During two trapping seasons I caught 991 individuals in 5,346 traps. Trapping success was 18.5 %. I trapped four different small mammal species with the most frequent species being *Praomys* cf. *jacksoni* with 925 individuals, and three species being less abundant (*Hylomyscus* sp. (42 ind.), *Lophuromys laticeps* (20 ind.) and *Crocidura* sp. (4 ind.). *Praomys* cf. *jacksoni* was the only species being present in all nine plots (Tab. 4.1). Characteristics of the four species caught are given in Tab. 4.2. Mean activity of small mammals in 1-ha plots (99 traps) ranged from 3-43 in the dry season and from 1-31 in the rainy season.

Table 4.1: Forest patches size and total number of the four small mammal species caught in the nine different plots.

Plot	Forest patch size (ha)	*Praomys* cf. *jacksoni*	*Hylomyscus* sp.	*Lophuromys laticeps*	*Crocidura* sp.
Malava	190	116	16	1	1
Kisere	420	19	2	-	-
Mukangu	8537	105	5	4	-
Buyangu	8537	53	-	-	-
Isecheno B	8537	155	11	-	-
Isecheno A	8537	97	1	-	-
Yala	1199	205	2	1	2
Ikuywa	1370	116	4	2	-
Kaimosi	130	51	-	-	-

Individuals of *Praomys* cf. *jacksoni, Hylomyscus* sp. and *Lophuromys laticeps* ate the seeds during the 24 h period in the cages and were therefore identified as seed predators

(own data and M. Melcher, unpublished data). I did not keep *Crocidura* sp. in the cages due to its high metabolism. Moreover, it is known as an insectivorous species. Therefore, I included only *Praomys* cf. *jacksoni, Hylomyscus* sp. and *Lophuromys laticeps* in the following analyses.

Table 4.2: Measurements (hb = head and body, t = tail, w = weight), geographic distribution and diet of the four small mammal species caught (from Kingdon 1997).

Species	Measurements			Distribution	Diet
	hb (cm)	t (cm)	w (g)		
Praomys cf. *jacksoni*	9-15	10-17	30-50	Gambia-Indian Ocean	omnivorous, invertebrates, fruits, seeds, leaves
Hylomyscus sp.	7-12	10-18	8-42	Guinea-East African Mountains	omnivorous, fruits, seeds, insects
Lophuromys laticeps	9-16	6-15	20-100	Tropical Africa	invertebrates, carrion, plant material
Crocidura sp.	45-140	45-90	11-40	Africa-wide	invertebrates, small vertebrates

The activity of seed predators did not differ significantly between fragments and main forest sites and between less and highly disturbed sites, neither in the dry nor in the rainy season (ANOVA type III SS: dry season: whole model: $F_{2,6} = 1.02$, $P = 0.41$, fragmentation: $F_{1,6} = 0.53$, $P = 0.49$, disturbance: $F_{1,6} = 1.95$, $P = 0.21$, $R^2 = 0.25$; rainy season: whole model: $F_{2,6} = 0.021$, $P = 0.97$, fragmentation: $F_{1,6} = 0.030$, $p = 0.87$, disturbance: $F_{1,6} = 0.025$, $P = 0.88$, $R^2 = 0.0069$; Fig. 4.2A, B). However, in the dry season there was a tendency towards more individuals being caught under the high than low disturbance regime (Figure 4.2A, B).

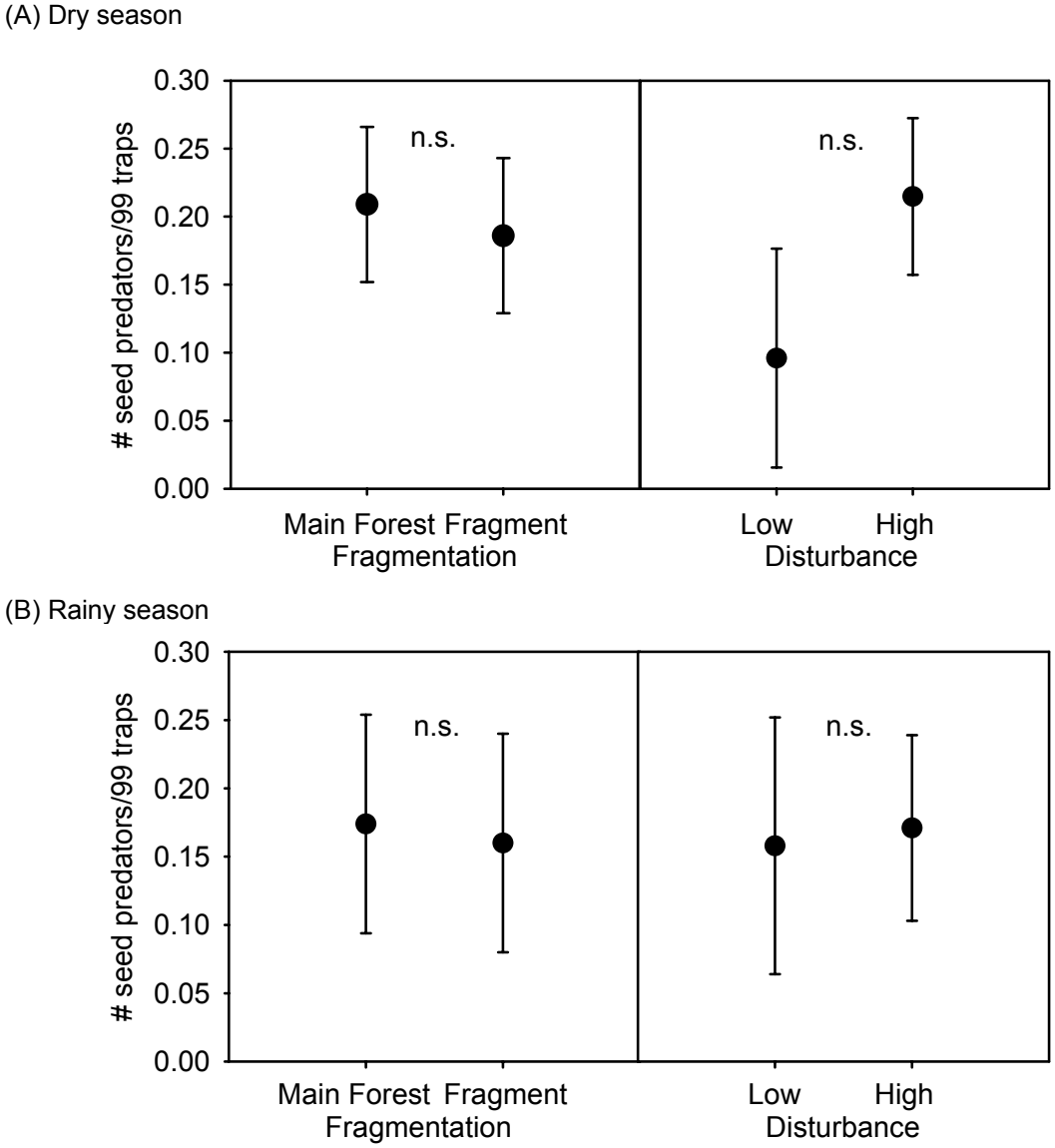


Figure 4.2: Number of seed predators caught in the **A** dry and **B** rainy season in relation to fragmentation (left) and disturbance (right). Given are least square means ± *SE*, ns = not significant.

4.3.2 Predation experiments

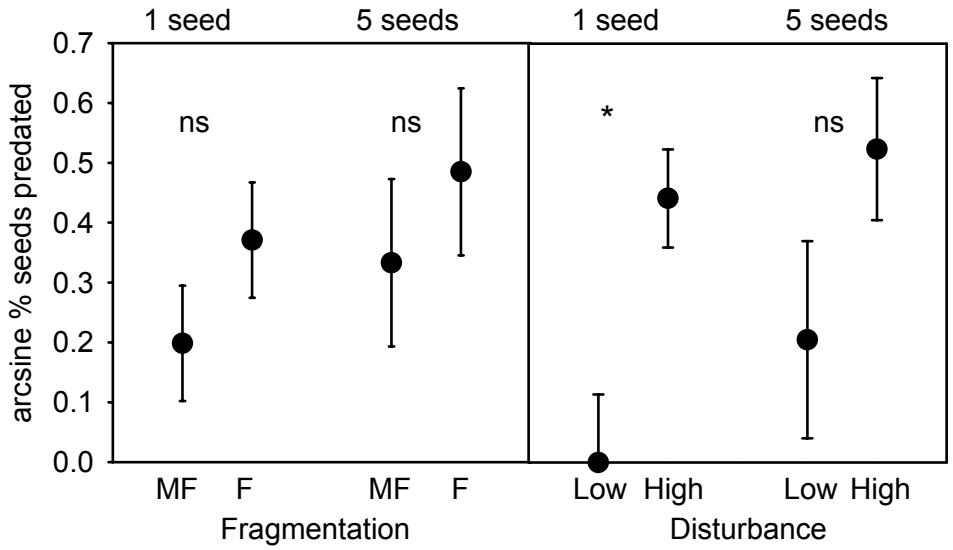
In all study plots the presence of urine, droppings and seed remnants indicated that small mammals were the major seed predators.

For the 1-seed dishes I found significantly more seeds preyed upon in highly disturbed sites than in less disturbed sites in the dry but not in the rainy season (ANOVA type III SS: dry season: whole model: $F_{2,6} = 5.29$, $P = 0.047$, fragmentation: $F_{1,6} = 0.11$, $P = 0.75$, disturbance: $F_{1,6} = 8.81$, $P = 0.025$, $R^2 = 0.64$; rainy season: whole model: $F_{2,6} = 2.18$, $P = 0.19$, fragmentation: $F_{1,6} = 0.41$, $P = 0.55$, disturbance: $F_{1,} = 2.83$, $P = 0.14$,

$R^2 = 0.42$; Fig. 4.3A, B). No difference was found between highly and less disturbed sites for the 5-seeds dishes, neither in the dry nor in the rainy season (ANOVA type III SS: dry season: whole model: $F_{2,6} = 1.35$, $P = 0.33$, fragmentation: $F_{1,6} = 0.10$, $P = 0.76$, disturbance: $F_{1,6} = 2.04$, $P = 0.20$, $R^2 = 0.31$; rainy season: whole model: $F_{2,6} = 1.15$, p = 0.38, fragmentation: $F_{1,6} = 0.27$, $P = 0.62$, disturbance: $F_{1,6} = 2.29$, $P = 0.18$, $R^2 = 0.27$; Fig. 4.3A, B). However, in the dry season there was a tendency for the 5-seeds dishes towards more seeds preyed upon in highly disturbed than in less disturbed sites (Figure 4.3A). Fragmentation did not have any effect on seed predation, neither for the 1-seed nor for the 5-seeds dish in any season (Fig. 4.3A, B).

In the dry season I found a marginally significant effect of density dependence with more seeds preyed upon from the 5-seeds dishes than from the 1-seed dishes (paired t-Test: $t = 2.22$, $P = 0.057$, $N = 9$). In the rainy season, significantly more seeds were preyed upon from the 5-seeds dishes than from the 1-seed dishes (paired t-Test: $t = 3.02$, $P = 0.017$, $N = 9$). When testing the degree of density dependence as a function of fragmentation and disturbance I found neither for the dry nor for the rainy season any fragmentation or disturbance effect (ANOVA type III SS: dry season: $P > 0.52$, rainy season: $P > 0.32$, respectively).

(A) Dry season



(B) Rainy season

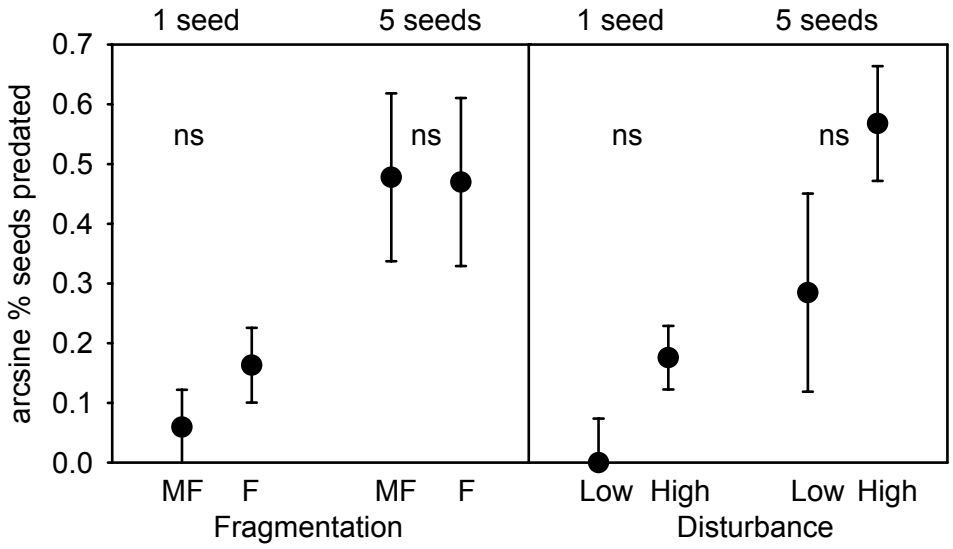
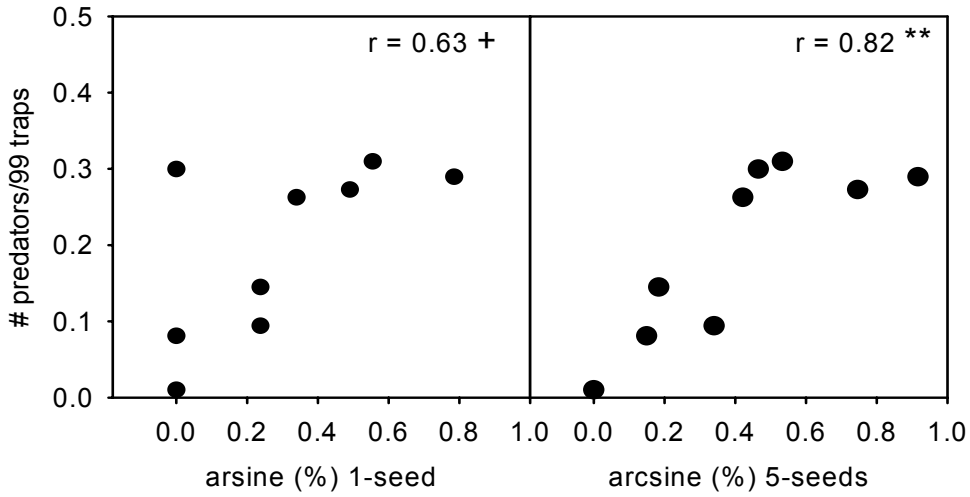


Figure 4.3: Percentage of seeds preyed upon for the 1-seed dish and the 5-seeds dish in the **A** dry and in the **B** rainy season in relation to fragmentation (left) and disturbance (right). Percentages were arcsine square root transformed (arcsin√p). Given are least square means ± *SE*, MF = Main Forest, F = Fragment, ns = not significant, **P* <0.05.

(A) Dry season



(B) Rainy season

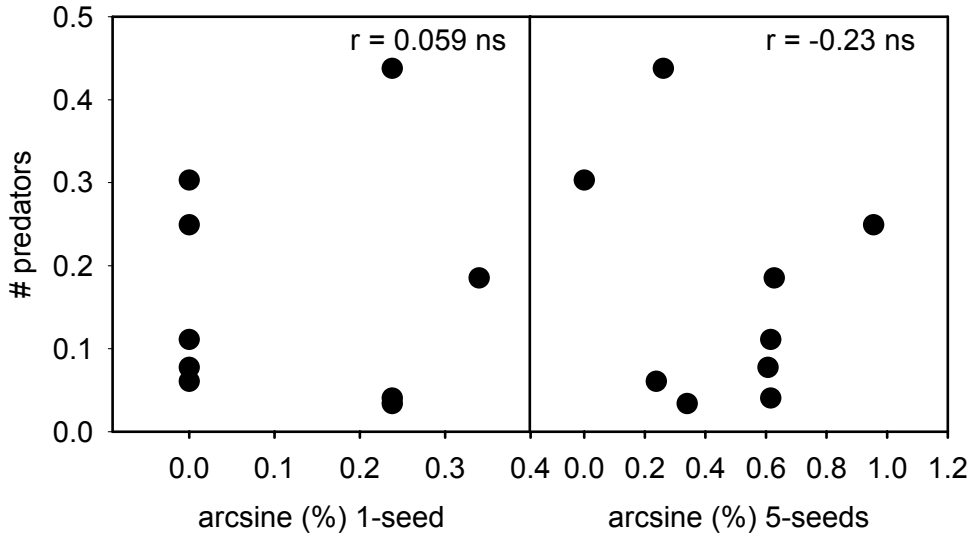


Figure 4.4: Correlation between number of predators and number of seeds preyed upon separately for the 1-seed dish (left) and the 5-seeds dish (right) in the **A** dry and in the **B** rainy season. Percentages were arcsine square root transformed (arcsin√p) prior to statistical analysis. Given are Pearson correlation *r*, ns = not significant, $^{+}0.05<P<0.1$, $^{**}P<0.01$.

When correlating the number of seed predators with the percentage of seeds preyed upon per plot in the dry season I found a marginally significant positive correlation between number of seed predators and percentage of seeds preyed upon on the 1-seed dish and a significant correlation between number of predators and seeds preyed upon on the 5-seeds dish (1-seed dish: Pearson correlation: $r = 0.64$, $P = 0.066$; 5-seeds dish: Pearson correlation: $r = 0.82$, $P = 0.0063$) (Fig. 4.4A). In the rainy season, I found neither a correlation between number of predators and percentage of seeds preyed upon for the 1-

seed dish nor between number of predators and percentage of seeds preyed upon for the 5-seeds dish (1-seed dish Pearson correlation: $r = 0.059$, $P = 0.88$; 5-seeds dish Pearson correlation: $r = -0.23$, $P = 0.55$) (Fig. 4.4B).

4.4 Discussion

I caught 991 individuals from four different small mammal species during two trapping seasons; three of them were confirmed as seed predators through feeding experiments. Functional diversity of small mammals (4-200 g) was low compared to other tropical forests with numbers ranging from four to 67 species (Harrington et al. 2001, Kasangaki et al. 2003, Nicolas and Colyn 2003, Suntsov et al. 2003). Waweru and Odanga (2004) recorded six additional small mammal species in regenerating but not in mature forest patches of Kakamega Forest. However, I caught two of those only in the adjacent agricultural farmland (data not shown). In a comparable montane forest in Uganda, Kasangaki et al. (2003) recorded 22 small small mammal species.

In addition to the three small mammals I identified as seed predators, other predators appear possible. Infrared camera traps baited with *P. africana* seeds, identified one other potential seed predator, *Cricetomys* sp., a 1-1.5 kg small mammal which is too large to be caught in the Sherman live-traps I used (M. Melcher, unpublished data). However, *Cricetomys* sp. has not been confirmed to feed on *P. africana* seeds and appears to be rare compared to the other species recorded with the infrared camera traps (*Cricetomys* sp. 5.2 %, *Praomys* cf. *jacksoni* 90.8 %, *Lophuromys* sp. 4.0 % of the pictures; M. Melcher, unpublished data). In addition, squirrels were often observed close to *P. africana* trees but never seen feeding on its fruits or seeds (personal observations). Potential larger seed predators could be Blue Duiker (*Cephalophus monticola*), Red Duiker (*Cephalophus harveyi*), Bushbuck (*Tragelaphus scriptus*) and Bush Pig (*Potamochoerus porcus*). However, they were not quantitatively assessed in this study and only occur in low densities in Kakamega Forest (Angwin 1980). Ground feeding birds such as thrushes and francolins could also be potential predators but have never been observed feeding on *P. africana* seeds.

Small mammals can act as both, secondary seed dispersers and seed predators, hence having either a positive or negative impact on seeds from the plant's perspective

(Forget 1996). Scatter-hoarding rodents that bury large numbers of seeds subsurface can provide some protection of seeds from predation pressure. They disperse seeds away from the parent plant and can enhance the germination ability below ground. However, small mammals that instantaneously feed on seeds act as predators and may reduce the number and viability of remaining seeds and thus the seedlings for regeneration. In my study the small mammal species seemed to act as predators rather than as secondary dispersers. The small mammals kept in the cages always preyed upon the seeds and were never observed to hoard them. Experiments with thread-marked *P. africana* seeds did not record any caching of seeds (M. Melcher, unpublished data). In addition, I did not find dense groups of seedlings away from adult *P. africana* trees which would be a sign of seedlings germinating from a scatter hoard.

I found neither a significant effect of fragmentation nor of disturbance on seed predator activity in the dry and in the rainy season. Nevertheless, there was a tendency towards more predators in highly than in less disturbed sites in the dry season. Single seeds had significantly higher predation rates in highly disturbed compared to less disturbed sites in the dry season. I did not detect any statistically significant interaction between fragmentation and disturbance effects. Overall, in a number of statistical tests effect size was quite large but not statistically significant (Fig. 4.2A, 4.3A). This lack of statistically significant effects might very well be due to the small sample size of only four plots in the main forest and five plots in fragments. However, an increase of sample size was not possible in this study because there are no more than the five fragments in the vicinity of Kakamega Forest. Furthermore, there are no other Afromontane rain forests left in Kenya in which a study, alternatively, could have taken place.

I always found a stronger influence of disturbance than of fragmentation. A possible reason for this pattern could be that disturbance changes the habitat on the same spatial scale as small mammals perceive their habitat. Existing studies showed that small mammals are dependent on a complex understory. It offers them a greater variety of microhabitat and better protection against predators (Hay and Fuller 1981, Kotler 1984, Kotler and Blaustein 1995). Furthermore, enhanced vegetative biomass may also cause an increasing quantity and quality of food and in turn provides better survival for larger populations of rodents (Simonetti 1989, Keesing 1998). I did not measure the understory vegetation in the different plots. However, plots in highly disturbed sites seemed to have a more complex understory (personal observations). A more complex understory might arise from better

light conditions (Levey 1988, b, Debinski and Holt 2000, Wenny 2001). I recorded such better light conditions in highly disturbed compared to less disturbed sites (B. Bleher, unpublished data).

In contrast to my results, Waweru and Odanga (2004) found higher numbers of *Praomys jacksoni* and *Hylomyscus stella* in the mature compared to regenerating forest in the fragment Kisere and the main forest site Buyangu of Kakamega. The contrary results could be explained by the fact that my highly disturbed sites are still less disturbed than transects in regenerating forests in the study of Waweru and Odanga (2004). Thus, the regenerating sites of Waweru and Odanga (2004) could be so severely disturbed that they appear to provide not enough resources to support large small mammal populations.

The missing effects of fragmentation could be due to the fact that small mammals have rather small home ranges which are smaller in size than the studied fragments. To reach another forest patch, i.e. a different fragment or the main forest block, small mammals would have to cross large distances through the adjacent farmland. Moreover, I did not trap my four small mammal species in the adjacent agricultural farmland (data not shown). Thus, they seem not to be able to cross wider gaps. Nevertheless, my results do not yet suggest a negative effect of fragmentation. The studied fragments seem to be still large enough to maintain sufficiently large small mammal populations.

I found a marginally significant effect of density dependence in the dry and a significant effect in the rainy seasons with a single seed having a higher probability of being eaten on the 5-seeds than on the 1-seed dish. This adds to other experimental studies showing that the probability that seed piles are discovered and seeds eaten by small mammals depend on seed density (Willson and Whelan 1990, Hulme 1994, Romo et al. 2004). Activity of small mammals correlated marginally with the predated seeds on the 1-seed dish and significantly with the predated seeds on the 5-seed dish in the dry season. This suggests a more or less linear relationship between small mammal activity and predation rates in the dry season.

With the results of the present study it is possible to compare the effects of forest fragmentation and disturbance on seed predation and seed dispersal in the same tree species. In the study on seed dispersal I recorded higher numbers of frugivores and slightly enhanced seed dispersal in fragmented and highly disturbed sites as compared to main forest and less disturbed sites in Kakamega Forest. The effects were stronger and statistically significant. Thus, the two processes in the life cycle of *P. africana* are to some

degree counteracting. Whereas the process of seed dispersal seems to be strengthened in highly fragmented and disturbed sites resulting in enhanced regeneration potential of *P. africana*, the subsequent process of seed predation shows trends towards higher predation rates in more heavily disturbed sites leading to diminished regeneration capability of the species. Thus, fragmentation and disturbance can have opposite effects on different processes in the life cycle of a tree. This demonstrates that extrapolation of the results from one process in the life cycle of a tree to another seems not to be possible. The next steps would be to investigate seedling establishment and survival of *P. africana* to predict whether or not the tree regenerates sufficiently and is able to maintain sustainable populations in Kakamega Forest. Only by studying all processes in the life cycle of a tree it is possible to develop sound conservation and management strategies for the species.

4.5 Summary

Anthropogenic forest fragmentation and disturbance can influence several processes in the life cycle of tropical tree species, such as e.g. pollination, seed dispersal and seed predation. However, rarely more than one of these processes has been studied in the same species. In a previous study on the influence of fragmentation and disturbance on seed dispersal of *Prunus africana* (Rosaceae) in the tropical rainforest of Kakamega, western Kenya, I found enhanced seed dispersal especially in fragmented and highly disturbed sites. To see whether this unusual pattern applies also to other processes in the life cycle of the tree, I studied the impact of fragmentation and disturbance on seed predation of *P. africana* in the same forest. I quantified the activity of small mammals in the main forest, forest fragments and differently disturbed sites in the dry and in the rainy season. Potential seed predators were identified through feeding experiments. Finally, I performed predation experiments with single and groups of *P. africana* seeds in the same sites. The results suggest that predation of *P. africana* seeds in Kakamega Forest was mainly caused by small mammals. I recorded a tendency towards higher activity of seed predators in highly disturbed compared to less disturbed sites in the dry season. Single seeds in contrast to groups of seeds of *P. africana* had significantly higher predation rates in highly disturbed compared to less disturbed sites, again only in the dry season. Thus, disturbance seems to increase seed predation rates of

P. africana, at least in one of the seasons. These findings demonstrate that fragmentation and disturbance can have contrary effects on different processes in the life cycle of a tree.

5 CONSEQUENCES OF FRAGMENTATION FOR THE GENETIC STRUCTURE OF POPULATIONS

5.1 Introduction

Tropical ecosystems suffered profoundly as a result of human over-exploitation (Chapin et al. 2000). Extensive deforestation led to the destruction of tropical forest forming the natural habitat of many species. Resultant habitat fragmentation threatens the survival of species (Aldrich and Hamrick 1998). Moreover, fragmentation has been shown to affect ecological processes and services such as pollination and seed dispersal (Chapin et al. 2000, Luck et al. 2003, Şekercioğlu et al. 2004). Consequences such as decreased pollination and seed output (Aizen and Feinsinger 1994), reduced seed removal (Cordeiro and Howe 2003), increased seed predation (Howe 1993) or reduced recruitment (Cordeiro and Howe 2001, 2003) may arise from loss of functional groups, e.g. pollinators and seed dispersers (Lundberg and Moberg 2003).

Pollination and seed dispersal are not only fundamental ecological processes and services but are also the two vectors for gene flow in plants and, thus, influence their genetic structure (Shapcott 1999, Pacheco and Simonetti 2000). Absence of genetic variance among individuals within and among populations suggests high levels of gene flow in previous generations. The genetic structure, i.e. the genetic differentiation within and between populations, is modified when gene flow by pollen and seed dispersal is limited. Forest fragmentation can lead to limited gene flow, causing increased inbreeding, and genetic drift decreasing the genetic diversity within populations (Young et al. 1996, Keller and Waller 2002). Decreased genetic diversity may imperil the adaptive potential and, as a consequence, fitness of populations and thus lead to extinction (McLaughlin et al.

2002). Analysing the levels and patterns of genetic structure in fragmented populations is crucial to understand the effects of habitat fragmentation on gene flow and for developing conservation strategies.

Studies on effects of fragmentation for the genetic structure of trees often revealed increasing differentiation among populations as a result of fragmentation. Most of these studies have been conducted across space comparing differently fragmented populations. For example, Hall et al. (1994) found limited gene flow in the tree *Pentaclethra macroloba* among sites in a fragmented terrain compared to sites within a continuous forest reserve. Prober and Brown (1994) were able to link levels of genetic variation to patch size in *Eucalyptus albens.* Only few studies have investigated the impact of forest fragmentation on gene flow over time. Due to the longevity of trees, one can gain a better understanding of patterns in gene flow by including not only adults but also seedlings or saplings into the study. In case fragmentation took place in between the time periods when adult trees and seedlings got established, patterns of genetic variation in adults might reflect gene flow before and in seedlings after fragmentation of the forest. In this case, gene flow among adult trees might have been intensive, whereas gene flow in the seedling generation could already be restricted.

One of the few studies investigating the genetic structure of tropical tree populations from a multistage perspective including adults, seedlings and saplings was carried out in a rain forest area and a series of smaller forest patches in Costa Rica (Aldrich et al. 1998). Significant inbreeding and genetic differentiation among patches were recorded for *Symphonia globulifera* only in the seedling stage of the fragmented forest patches (Aldrich et al. 1998). A study on *Carapa guianensis* revealed lower allelic richness and greater genetic distances among the sapling cohort than the adult population in an isolated managed forest suggesting restriction of gene flow due to deforestation and habitat fragmentation (Dayanandan et al. 1999).

In the present study, I investigated the genetic structure of adult trees and seedlings of *Prunus africana* (Rosaceae) using six microsatellite markers. I explicitly sampled adults and seedlings which allowed studying changes in the pattern of gene flow between generations. Wild populations of *P. africana* have been declining over much of their geographical range in sub-Saharan African due to the over-exploitation of their medicinally valuable bark (Cunningham and Mbenkum 1993). My study area was Kakamega Forest, an Afromontane rainforest consisting of a continuous forest block and several fragments,

where a recent study on *P. africana* revealed a rapid decline of the species (Fashing 2004). I assume that adults represent the historical pattern of gene flow in Kakamega forest, possibly only slightly influenced by starting forest fragmentation, whereas seedlings show the present pattern in gene flow, 55-100 years after forest fragmentation (Mitchell 2004). To examine the spatial genetic structure within and among fragmented and continuous forest I addressed the following questions: (i) does genetic structure exist among adult trees? And (ii) how does human-induced habitat fragmentation affect the genetic structure among seedlings?

5.2 Material and methods

5.2.1 Study species

Prunus africana Hook f. (Rosaceae) is an evergreen tree species native to Africa and Madagascar typical of mature climax forests (Kalkman 1965). The monoecious tree grows up to 40 m in height producing small white flowers in elongated clusters which are basically insect pollinated (personal observations). It has purple fleshy one-seeded fruits (seeds: diameter: 6.6 ± 0.5 mm, mass: 0.15 ± 0.05 g, $N = 30$) which are dispersed by birds and monkeys (see chapter 3). *Prunus africana* belonged to the group of species which has been intensively logged in all parts of Kakamega forest (Mitchell 2004, see below).

5.2.2 Study site

The study was conducted in Kakamega Forest, western Kenya (between latitudes 0°14’ and 0°21’N and longitudes 34°47’ and 34°48’E). Kakamega Forest is the eastern most relict of the Guineo-Congolian rainforest belt and lies at an altitude of 1,500 to 1,700 m asl. (Kokwaro 1988). It is a highly fragmented and disturbed montane tropical rainforest (Tsingalia 1990, Mitchell 2004). Average annual temperature of the forest lies between 10.6° and 27.7°C (Tsingalia 1990). Annual precipitation averages 2,007 mm and is highly seasonal with a rainy season from April to November and a short dry season from December to March (as averaged from Forest Department records at Isecheno Forest Station from 1982 to 2001).

The indigenous forest cover of Kakamega is reported to have been reduced from 23,785 ha in 1933 to 13,990 ha in about 1990 (Blackett 1994). Most clear-felling was conducted in the southern part of the forest and along the western fringe close to the city of

Kakamega (Mitchell 2004). Clear-felling has not only destroyed half of the forest but also resulted in fragmentation of the forest (Fig. 5.1). Presently, the forest covers an area of 8,500 ha of a main forest block surrounded by five forest fragments of various sizes (130–1,400 ha), Malava and Kisere in the north, and Yala, Ikuywa and Kaimosi in the south (Fig. 5.1). We treat Yala and Ikuywa as two different fragments because they are separated by a road dividing the narrow strip of forest still connecting the fragments. The fragments Malava and Kisere in the north have either never been connected to the other parts of the forest in historical times (Mitchell 2004) or have been isolated from the other parts of the forest for at least the last 100 years (Brooks et al. 1999). In contrast, the fragment Kaimosi in the south has been separated from the main forest between 1913-1959 and the fragments Yala and Ikuywa since the early 1960s (Mitchell 2004). The forest is surrounded by a densely settled agricultural area (600 people/km^2; KIFCON 1994) which is composed of small patches of fields planted with sugarcane, maize, beans or tea interspersed by single large forest trees and small shrubs. Further information on the fragmentation and disturbance history of Kakamega Forest is given in Tsingalia (1990), Mitchell (2004) and Bleher et al. (in press).

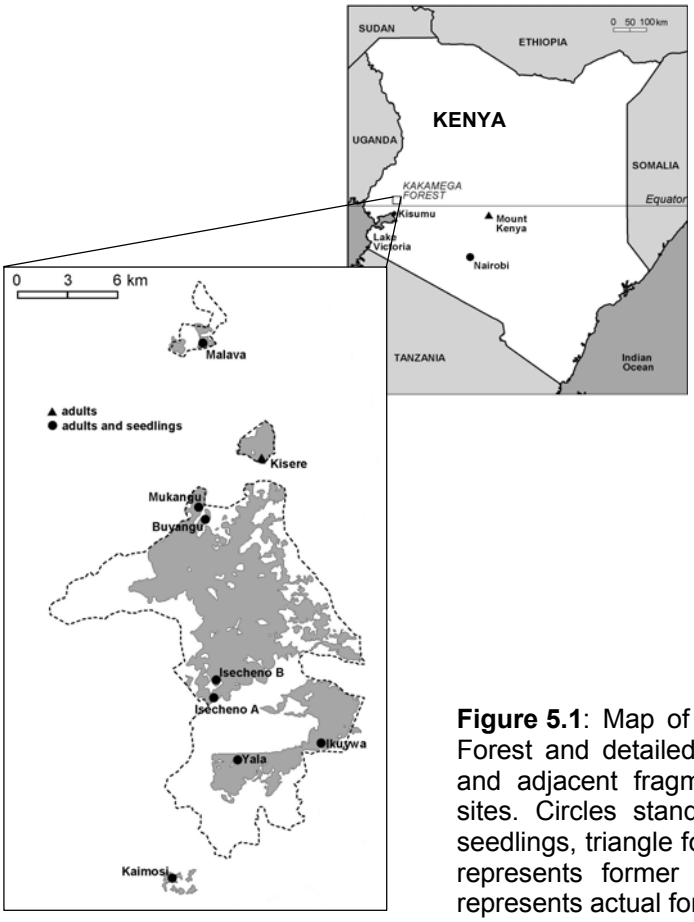


Figure 5.1: Map of Kenya indicating location of Kakamega Forest and detailed map of Kakamega Forest: Main forest and adjacent fragments with location of the nine sample sites. Circles stand for sample sites of both, adults and seedlings, triangle for sample site of adults only. Dashed line represents former forest boundary (1933), grey shading represents actual forest cover. Courtesy of G. Schaab.

5.2.3 Plant material

In June 2002 I collected leaf material of adult trees and seedlings of *P. africana* in nine different sites of Kakamega Forest, four sites in the main forest block (two in the north and two in the south) and five in fragments with one in each of the five forest fragments Malava, Kisere, Ikuywa, Yala and Kaimosi (Fig. 5.1). In each site I randomly sampled 7-14 adult trees (80-100 years old) and in all sites, except the fragment Kisere, 3-13 seedlings (1-5 years old) 5-7 m away from the tree crown of the sampled adult trees. By sampling seedlings a minimum distance away from the adult trees I wanted to ensure that seedlings had a low probability of being related to the sampled adults and that we obtained a random sample of each generation per site. In total, 93 adult and 58 seedling individuals were sampled. Considering the age of the adult trees, I assume that adult trees got established before the three southern fragments Ikuywa, Yala and Kaimosi were separated among themselves and from the main forest. Note that the northern fragments, Malava and Kisere, might have been separated from the main forest before the adult trees got established as seedlings. In contrast, the seedlings represent the present distribution of forest (Fig. 5.1). Plant material was silica-dried in the field. For statistical analyses, each site was defined as a single population.

5.2.4 Molecular analysis

Leaves were ground to a fine powder in liquid nitrogen using a mortar and pestle. DNA was extracted from the powder of ~1.0 g leaf material of *P. africana*, following the protocol described in DNEASY Plant Mini Kit (QUIAGEN). The standard protocol was slightly modified by using 500 µl buffer AP1 and 160 µl buffer AP2 which handled the amount of leaf material better. DNA was stored at -20°C in AE (QUIAGEN) elution buffer.

I studied the levels of genetic variation using six microsatellite marker loci, four listed by Cipriani et al. (1999) and two listed by Sosinski et al. (2000). The forward and reverse primers for each microsatellite locus are presented in Table 5.1. Instead of radioactive labelling we used fluorescent ‘E’-primers (6-FAM, NED, HEX, Applied Biosystems, ABI).

Polymerase chain reactions (PCR) were performed in a volume of 25 µl containing 10 mM Tris-HCl (pH 9.0), 50 mM KCl, 1.5 mM $MgCl_2$, 4 x 0.2 mM dNTP, ~1.5 units Taq polymerase (Ready-To-Go™ PCR-Beads, Amersham Pharmacia Biotech Inc.), primer ranging from 2*0.07 to 2*0.5 µl (the forward primer of each pair was fluorescent ‘E’

marked), respectively, aqua bidest ranging from 23.86 to 22.7 µl, respectively, and 1 µl genomic DNA using the following temperature profile: 95°C for 5 min, then 35 cycles of (94°C for 45 s, 60-62°C for 45 s and 72°C for 45 s), finishing with 72°C for 8 min. Primers U1 and U5, P2 and U3 were performed in multiplex PCR. All pipeting was done with a lab robot (RoboSeq 4204 SE, MWG).

Table 5.1: Primer sequences and repeat motif listed by Cipriani et al. (1999) and Sosinski et al. (2000). Range of PCR product sizes, annealing temperature and primer concentration of the six microsatellites used in this study. Primer U1 and U5, U3 and P2 were performed in multiplex PCR.

Locus code	Primer sequences	Repeat motif	Length (bp)	Annealing temp.	Primer concentration
U1 (UDP96-001)	AGTTTGATTTTCTGATGCATCC TGCCATAAGGACCGGTATGT	(CA)17	86-146	60 °C	5.0 pmol/µl
U2 (UDP98-406)	TCGGAAACTGGTAGTATGAACAGA ATGGGTCGTATGCACAGTCA	(AG)15	73-123	60 °C	0.7 pmol/µl
U3 (UDP97-403)	CTGGCTTACAACTCGCAAGC CGTCGACCAACTGAGACTCA	(AG)22	119-155	60 °C	1.0 pmol/µl
U5 (UDP96-018)	TTCTAATCTGGGCTATGGCG GAAGTTCACATTTACGACAGGG	(AC)21	238-258	60 °C	1.5 pmol/µl
P1 (pchcms5)	CGCCCATGACAAACTTA GTCAAGAGGTACACCAG	(CA)9(TA)8	241-193	62 °C	0.3 pmol/µl
P2 (PS12A02)	GCCACCAATGGTTCTTCC AGCACCAGATGCACCTGA	(GA)21	133-195	62 °C	3.0 pmol/µl

The labelled PCR products were separated on a 4.5 %-polyacrylamid gel automatic sequencer as a multiplex of one or two differently labelled products together with one internal size standard (GENESCAN ROX 500, ABI). Gels were run for 3 hrs on an ABI 377 automated sequencer, and allele sizes were determined using GENESCAN analysis software (version 2.1. ABI). Peaks were scored automatically with GENOTYPER analysis software (version 3.1. ABI) and crosschecked visually.

5.2.5 Data analysis

The mean number of alleles per locus and site, allele frequencies, the observed heterozygosity H_O and the expected heterozygosity H_E (Nei 1978) in both stage classes (adults, seedlings) were computed using TFPGA (Tools for population genetic analysis, Miller 1997). Genotypic linkage disequilibria between pairs of loci and departures from Hardy-Weinberg equilibrium at each locus were tested using GENEPOP 3.4 software (Raymond and Rousset 1995a). F-statistics for all loci was calculated using SPAGeDi (Spatial Pattern Analysis of Genetic Diversity, Hardy and Vekemans 2002). The number of

migrants for all loci was calculated according to the formula $Nm = 0.25\ (1\text{-}F_{ST})/F_{ST}$ (Slatkin 1993).

To examine the relative partitioning of genetic variation within and among sites a hierarchical analysis of molecular variance (AMOVA) was calculated with ARLEQUIN Version 2.000 (Schneider et al. 2000). To test whether fragmentation affected gene flow I grouped the populations of the four main forest sites together as one group, and treated the five forest fragments (Malava, Kisere, Yala, Ikuywa, Kaimosi), containing each only a single population, as five separate groups. With this design, the variation among the six groups represented the variation among fragments and between fragments and the main forest group, the variation among populations within groups stood for the variation between the four main forest populations and the variation within populations accounted for the variation between individuals within populations. For each pair of populations I estimated pairwise F_{ST}-values for population differentiation determined after 110 permutations (Raymond and Rousset 1995b). To test for isolation by distance (IBD) at the scale of the populations, I regressed $F_{ST}/1\text{-}F_{ST}$, based on pairwise F_{ST}-values among all sampled populations, against the log-transformed geographic distance separating the populations (Slatkin 1993, Rousset 1997). Statistical significance was evaluated with a Mantel-test using 20,000 permutations, as implemented in TFPGA (Miller 1997).

A problem for the results of the statistical analyses might pose the fact that sample size for adults ($N = 93$) was larger than for seedlings ($N = 58$) and that adults were sampled from nine and seedlings from eight populations. To test whether results were influenced by sample size and number of populations, I repeated the analyses of adults with 10 random subsets of 58 individuals from the eight populations that were also represented by seedlings. When taking the random subsets, the number of adults drawn from each population corresponded to the number of seedlings sampled in the respective population. In cases, in which results were similar for 93 and 58 individuals, I report only the results for the complete sample. In cases where results differed, I present the results of both.

5.3 Results

5.3.1 Descriptive population genetics of adults and seedlings

All of the 93 samples of adult trees and 58 seedlings were clearly genotyped at the six microsatellite loci. Most results of the descriptive population genetics differed for the

analysis of 93 and 58 adults, so first the results for the complete sample, and, in parenthesis, the mean of 10 random subsets of 58 adults are presented. The loci were highly polymorphic with 98 alleles in the six loci, 94 (83) of them in adults and 73 of them in seedlings (mean number of alleles per locus over all populations 20.2 (14.0) and 12.2, respectively). The number of alleles varied between populations ranging from 37 to 54 (23-49) over six loci in adults and from 15 to 40 over six loci in seedlings. The mean number of alleles per population was significantly higher for adults than for seedlings (adults: 43.7 (35.2), seedlings: 29.9, Wilcoxon Matched Pair Signed Rank test ($N = 7$): $S = 18$, $P = 0.008$ ($S = 18$, $P = 0.008$)) (Table 2). The frequencies for individual alleles per population ranged from 0.042-0.64 (0.039-0.66) in adults and from 0.039-0.75 in seedlings. Observed heterozygosity H_O and expected heterozygosity H_E per population were always higher in adults than in seedlings (H_O: adults: 0.73-0.82 (0.69-0.77), seedlings: 0.50-0.71, WMPSR test ($N = 7$): $S = 17$, $P = 0.016$ ($S = 18$, $P = 0.008$); H_E: adults: 0.76-0.90 (0.75-0.82), seedlings: 0.60-0.79; WMPSR test: $S = 18$, $P = 0.008$ ($S = 15$, $P = 0.039$)) (Table 5.2). The summary of F-statistics (F_{IS}, F_{IT}, F_{ST}) over all loci showed always lower F_{ST}-values for adults compared to seedlings and in turn the estimated number of migrants (Nm) decreased from adults (10.7) to seedlings (3.3) (Table 5.3; results were similar for $N = 58$ adults).

Table 5.2: Number of samples, mean number of alleles per population, mean observed heterozygosity H_O and Nei's mean expected heterozygosity H_E for the six loci in nine populations for adults and in eight populations for seedlings of P. africana (TFPGA).

Plot	# samples		mean # alleles		H_O		H_E	
	adults	seedlings	adults	seedlings	adults	seedlings	adults	seedlings
Malava	9	5	7.2	4.7	0.74	0.70	0.81	0.77
Kisere	10	-	7.8	-	0.75	-	0.81	-
Mukangu	10	4	6.5	4.3	0.68	0.67	0.78	0.76
Buyangu	12	5	7.8	4.8	0.79	0.71	0.81	0.79
Isecheno B	14	13	7.2	6.0	0.75	0.70	0.76	0.73
Isecheno A	12	12	7.3	6.7	0.68	0.69	0.82	0.72
Yala	7	3	6.2	2.5	0.71	0.50	0.79	0.60
Ikuywa	11	10	9.0	5.5	0.74	0.66	0.82	0.69
Kaimosi	8	6	6.5	5.3	0.77	0.70	0.79	0.76

Table 5.3: Summary of F-statistics (F_{IS}, F_{IT}, F_{ST}) for all six loci of adults and seedlings of *P. africana* calculated with SPAGeDi and number of migrants.

Locus	F_{IS}		F_{IT}		F_{ST}		Nm	
	adults	seedlings	adults	seedlings	adults	seedlings	adults	seedlings
all loci	0.103	0.267	0.082	0.212	0.023	0.070	10.67	3.33
1	-0.055	0.215	-0.079	0.184	0.022	0.038	10.96	6.43
2	0.064	0.405	0.044	0.351	0.021	0.084	11.54	2.73
3	-0.075	0.073	-0.095	0.037	0.018	0.037	13.41	6.47
4	0.135	0.065	0.132	-0.098	0.002	0.148	103.92	1.43
5	-0.118	0.099	-0.123	0.054	0.004	0.047	62.25	5.04
6	0.662	0.696	0.641	0.666	0.060	0.091	3.92	2.51

5.3.2 Linkage and Hardy-Weinberg equilibrium of adults and seedlings

No linkage disequilibrium was detected between any pair of loci (non-significant after sequential Bonferroni correction, Rice 1989). All population-locus combinations were in Hardy-Weinberg equilibrium, except for the following combinations (significant after sequential Bonferroni correction, Rice 1989): Adults: Malava-locus6, Kisere-locus6, Mukangu-locus6, Isecheno B-locus6, Isecheno A-locus2, Isecheno A-locus6, Yala-locus6, Ikuywa-locus6, Kaimosi-locus6 ($N = 58$ individuals: Isecheno B-locus6, Isecheno A-locus2, Isecheno A-locus6); Seedlings: Isecheno B-locus6, Isecheno A-locus6, Kaimosi-locus1, Kaimosi-locus6 (all heterozygosity deficits). This heterozygosity deficit might be explained by spatial Wahlund effects but no sub-structuring could be detected within each of the sites. Likewise, a temporal Wahlund effect, i.e. subunits of individuals reproducing at different times (Morand et al. 2002), seems unlikely as F_{IS}-values were mostly higher than F_{ST}-values (Table 5.3). However, individual trees bred at slightly different times over the year (B. Bleher, unpublished data). Such heterozygosity deficit might also be caused by inbreeding in some forest fragments. If so, a deficit would be expected for all loci, which was not the case in my study. Alternatively, a heterozygosity deficit can result from the lack of amplification of some alleles (null alleles). The presence of null alleles particularly in locus6 causing most population-locus Hardy-Weinberg disequilibria and showing the highest F_{IS}-values cannot be discounted.

5.3.3 Genetic structure of adults and seedlings

The results of the genetic population structure were similar for $N = 93$ and $N = 58$ adult individuals. Thus, for all analyses only the results for the complete sample are presented. The overall F_{ST}-value for adults was 0.026 indicating low levels of genetic differentiation

and high levels of gene flow between sites (Table 5.4). Overall, F_{ST} for seedlings averaged 0.086 indicating higher levels of genetic differentiation between sites than for adults (Table 5.4).

Table 5.4: Analysis of molecular variance (AMOVA) conducted with ARLEQUIN for the nine adult and the eight seedling populations of *P. africana*.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Adults				
Among groups	5	17.556	0.0000	0.00
Among populations within groups	3	12.588	0.0753	3.05
Within populations	177	424.404	2.3978	96.96
Total	185	454.548	2.4619	
Seedlings				
Among groups	4	20.578	0.0088	2.52
Among populations within groups	3	13.569	0.1475	6.12
Within populations	108	237.948	2.2032	91.36
Total	115	272.095	2.4116	

Adults: Fixation indices: F_{ST} = 0.026, F_{SC} = 0.030, F_{CT} = 0.00; Seedlings: Fixation indices: F_{ST} = 0.086, F_{SC} = 0.063, F_{CT} = 0.025

The results of the hierarchical analysis of molecular variance (AMOVA) revealed for adults as well as for seedlings that most of the genetic variation was found within populations (~ 97 % and ~ 91 %, respectively, Table 5.4). The analyses showed no variation among groups (i.e., among fragments or between fragments and the main forest) for adults, but 2.5 % for seedlings. Variation among populations within groups (i.e., among the main forest sites) was 3 % for adults and 6 % for seedlings.

Pairwise F_{ST}-values showed higher differentiation between populations in seedlings (range 0.0-0.15) than in adults (range 0.0-0.072) (Table 5.5A, B). In adults significant differentiation was found in 18 of the 36 pairwise comparisons, and mainly between the southern populations (Table 5.5A). In seedlings, 24 of the 28 pairs of populations were significantly different (Chi²-test (N = 64): *Chi²-value* = 8.91, *D.F.* = 1, P = 0.0028, Table 5.5B).

Table 5.5A: Pairwise F_{ST}-values and their significance (lower left site of diagonal) and geographic distances in m (upper right site of diagonal) among the nine populations for adults of *P. africana*; **P*<0.05, ns = not significant (*P*>0.05).

Population	Malava	Kisere	Mukangu	Buyangu	Isecheno B	Isecheno A	Yala	Ikuywa	Kaimosi
Malava		8647.5	10813.0	11647.1	22543.3	23645.0	27690.1	27721.9	35644.3
Kisere	0.018 ns		5153.7	5456.1	15239.3	16372.6	19297.6	20076.0	28625.7
Mukangu	0.022 ns	0.002 ns		901.0	11744.2	12838.3	17583.3	16967.3	24859.7
Buyangu	0.030 *	0.004 ns	0.018 ns		10896.7	11998.3	16683.9	16100.8	24068.5
Isecheno B	0.042 *	0.016 ns	0.020 *	0.040 *		1133.4	8071.5	5297.7	13386.8
Isecheno A	0.008 ns	0.013 ns	0.002 *	0.011 ns	0.043 *		7792.5	4323.4	12253.6
Yala	0.030 ns	0.016 ns	0.036 ns	0.014 ns	0.072 *	0.034 *		5665.1	13441.2
Ikuywa	0.003 ns	0.000 ns	0.017 ns	0.021 *	0.020 ns	0.002 ns	0.036 *		9088.2
Kaimosi	0.041 *	0.031 *	0.017 *	0.044 *	0.056 *	0.052 *	0.053 *	0.037 *	

Table 5.5B: Pairwise F_{ST}-values and their significance (lower left site of diagonal) and geographic distances in m (upper right site of diagonal) among the eight populations for seedlings of *P. africana*; * *P*<0.05, ns = not significant (*P*>0.05).

Population	Malava	Mukangu	Buyangu	Isecheno B	Isecheno A	Yala	Ikuywa	Kaimosi
Malava		10813.0	11647.1	22543.3	23645.0	27690.1	27721.9	35644.3
Mukangu	0.109 *		901.0	11744.2	12838.3	17583.3	16967.3	24859.7
Buyangu	0.134 *	0.000 ns		10896.7	11998.3	16683.9	16100.8	24068.5
Isecheno B	0.135 *	0.080 *	0.080 *		1133.4	8071.5	5297.7	13386.8
Isecheno A	0.110 *	0.046 *	0.069 *	0.058 *		7792.5	4323.4	12253.6
Yala	0.148 *	0.114 *	0.152 *	0.124 *	0.102 *		5665.1	13441.2
Ikuywa	0.131 *	0.039 ns	0.060 *	0.083 *	0.035 *	0.067 ns		9088.2
Kaimosi	0.120 *	0.041 ns	0.094 *	0.049 *	0.054 *	0.127 *	0.101 *	

A test for isolation by distance resulted in no correlation for adults (Pearson correlation: $r = -0.01$, Mantel $P = 0.51$, $N = 9$, Fig. 5.2A). In contrast, seedlings showed a significant correlation of the genetic distance with the geographic distance (Pearson correlation: $r = 0.53$, Mantel $P = 0.012$, $N = 8$, Fig. 5.2B). Moreover, the genetic variance increased from adults to seedlings. While genetic distance of geographically close-by populations increased only slightly, geographically isolated populations differentiated to a higher degree (Fig. 5.2A, B).

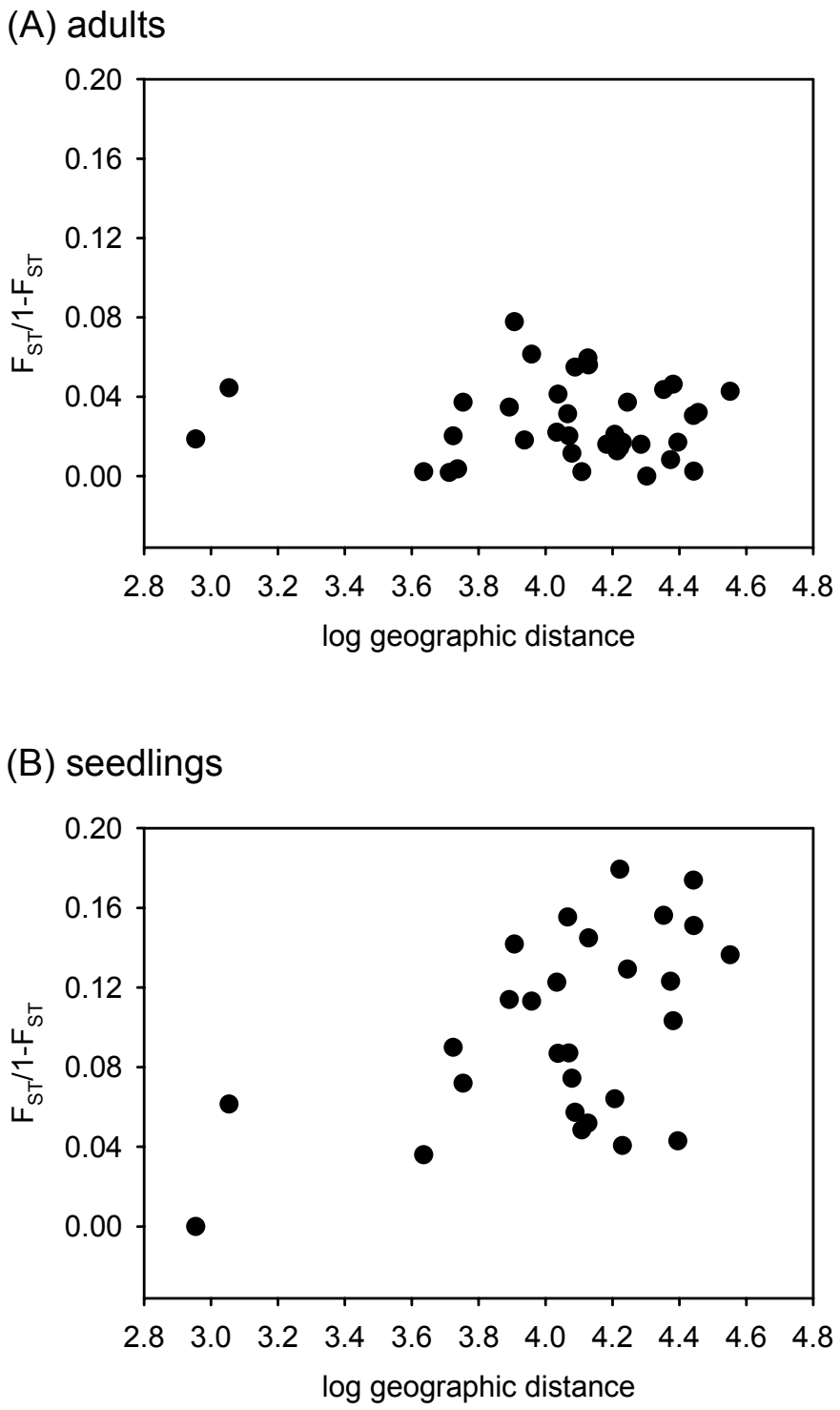


Figure 5.2: Genetic distance $F_{ST}/1- F_{ST}$ against geographic distance (m log transformed) among **A** nine populations for adults, and **B** eight populations for seedlings.

5.4 Discussion

5.4.1 Genetic structure of adults

My results showed high levels of allelic diversity in populations of *P. africana* adults combined with high levels of heterozygosity indicating a predominantly outcrossing species. This corresponds to field observations demonstrating that self-pollinated flowers did not develop fruits (personal observations). *P. africana* showed much higher values for heterozygosity in the present study (H_E = 0.76-0.90) than in an African-wide *P. africana* study using RAPDs (H_E = 0.067 for Kenya; Dawson and Powell 1999). The lower values for the RAPD study could be explained by using a different marker system. However, Belaj et al. (2003) compared the discriminating capacity of different marker systems and revealed only slight differences in the expected heterozygosity between RAPDs and microsatellites (0.28 and 0.42, respectively). Moreover, Russell et al. (1997) scored almost identical levels of expected heterozygosity in microsatellites and RAPDs in a study on genetic variation among barley accessions (0.57 and 0.52, respectively). Therefore, a more likely reason for the differences could be that Dawson and Powell (1999) studied isolated, remnant trees in farmland around Mt. Kenya which might have lost genetic diversity. Moreover, their study area, Mt. Kenya, is much more isolated from the former Guineo-Congolian rainforest belt than Kakamega forest. My results, therefore, suggest that *P. africana* populations in Kakamega Forest comprise a surprisingly high amount of genetic diversity given the isolated "position" of Kakamega forest ~ 600 km from the remaining Guineo-Congolian rainforests and given its severe fragmentation history.

Prunus africana exhibited weak genetic structure in adults (F_{ST} = 0.026). Low F_{ST}-values are found for most tree species (Hamrick and Godt 1997). This can be explained by a combination of the life history traits (long-lived, woody plants) and breeding system (outcrossing insect-pollinated flowers, animal-dispersed seeds) of most studied trees (Hamrick and Godt 1997, Jordano and Godoy 2000). Trees have long generation cycles and overlapping generations fostering little or no genetic structure among populations (Knowles 1991, Xie and Knowles 1991). The majority of tropical rainforest tree species that are outcrossers showed extensive gene flow in terms of pollen and seed movement (Doligez and Joly 1997, Nason and Hamrick 1997). Extensive gene flow via seeds has, for instance, been demonstrated in *Syzygium nervosum* (Shapcott 1999) and *Prunus mahaleb* (Godoy and Jordano 2001). However, the F_{ST}-value for adults in the present study was much lower

than the mean value for trees of F_{ST} = 0.2 as calculated by Hamrick and Godt (1997). This suggests especially high levels of gene flow via pollen and seed dispersal among populations in *P. africana* in the past. However, also two other studies on tropical trees revealed rather low F_{ST}-values ranging between 0.003 and 0.063 (e.g. Pacheco and Simonetti 2000, Cespedes et al. 2003). The authors explain the low F_{ST}-values by loss of rare alleles rather than loss of genetic diversity due to fragmentation and severe bottlenecks. Since genetic diversity is measured by allele frequencies, common alleles have a higher contribution to diversity than uncommon and rare alleles. Therefore, the loss of uncommon and rare alleles hardly affects diversity (Giles and Goudet 1997, Lawrence and Marshall 1997). In my study alleles found only in few populations were mostly present in low frequencies.

The lack of genetic structure in adults is congruent with the fragmentation history of Kakamega forest which started about 100 years ago (Mitchell 2004). I assume that the establishment of adults took place when the forest was still contiguous and extensive gene exchange could take place. Surprisingly, populations of Malava and Kisere which have either never been connected to the main forest in historical times or have been separated for at least the last 100 years show little differences to main forest populations. Historic data suggest that the land to the north of Kakamega main forest was only thinly populated by humans about 100 years ago (Mitchell 2004). Furthermore, in these times, the northern parts of the main forest and the fragments Malava and Kisere were probably connected via riparian forest corridors and a multitude of trees (Mitchell 2004) that might have been stepping stones especially for birds acting as seed dispersers. In contrast, populations of the southern fragments are very different from one another, in particular the population of Kaimosi which differs from all other populations. I cannot provide an explanation for this unexpected result.

5.4.2 Comparison between adults and seedlings

Comparing allelic diversity between adults and seedlings showed that allelic diversity decreased significantly from adults to seedlings indicating constant gene flow in the past and more limited gene flow in the present. The same pattern was found for the observed heterozygosity H_O and the expected heterozygosity H_E per population which were always higher in adults than in seedlings indicating genetic impoverishment of the seedling stage.

Furthermore, the comparison between adults and seedlings revealed higher genetic differentiation among populations in seedlings than in adults (F_{ST} = 0.086 versus 0.026). Reduced gene flow is also supported by the AMOVA, which showed an increase of genetic variation among groups (i.e., among fragments or between fragments and the main forest) from 0 % to 2.5 % from the adult to the seedling stage. Moreover, the AMOVA revealed an increase of genetic variation among populations within groups (i.e., among the four main forest sites) from 3 % in adults to 6 % in seedlings. This demonstrates that gene flow appears to be limited not only among the forest fragments but also among sites within the continuous main forest. Additionally, results from pairwise F_{ST}–values showed higher differentiation among populations in seedlings than in adults. Finally, when correlating the genetic distance among populations with their geographic distance, I found a clear IBD pattern for seedlings but not for adults. All these factors alone and in combination indicate a change of genetic population structure in the past 80-100 years. While the genetic structure of the adults seems to mirror the historic pattern of gene flow, the pattern for seedlings seems to reflect the present situation and suggests that forest fragmentation restricted gene flow in *P. africana*.

This pattern could be caused on the one side by increased fragmentation and reduced gene flow among populations. On the other side the pattern might be influenced by the number of individuals and populations from which samples had been taken (Whitlock and McCauley 1999). I, therefore, repeated the analyses for adults with random samples of 58 individuals from the eight populations also represented as seedlings. The results were all very similar and suggest that the pattern seems to be caused by a real difference in population genetic structure between adults and seedlings.

One explanation for the increasing differentiation of populations from the adult to the seedling generation particularly on this regional scale is the loss of pollinators or seed dispersers and, hence, diminished pollen or seed transport. For genetic exchange between the fragments in my study area, distances between 4.5 and 13.5 km need to be covered by pollinators or seed dispersers. To cover such distances is rather unlikely for the insect pollinators (bees and flies). In contrast, long-distance movements are known for many bird species, especially for large disperser such as hornbills (Holbrook and Smith 2000, Holbrook et al. 2002). Thus, I expect that the reduced genetic exchange in my study was caused rather by diminished seed dispersal, especially through large-bodied seed dispersers, than by diminished pollen transport.

A relationship between limited seed dispersal and increased population genetic structure has been shown in a number of studies. For example, a comparative study on the tropical tree *Inga ingoides* revealed more differentiation among subpopulations where the spider monkey as seed disperser was absent than where it was present (Pacheco and Simonetti 2000). Furthermore, the results showed that in the absence of spider monkeys family genetic structure increased in the first generation of seedlings which should accelerate the development of population genetic structure (Pacheco and Simonetti 2000). Limited seed dispersal was related to a stronger genetic structure among populations also in other tree species (Perry and Knowles 1996, Ueno et al. 2000).

If the reduced genetic exchange was caused by the loss of seed dispersers I might expect poor visitation and seed dispersal rates of fruiting *P. africana* trees especially in forest fragments. However, there is no evidence for reduced visitation or seed dispersal rates of trees in fragments in my study system. Quite in contrast, *P. africana* trees are presently visited by a diverse frugivore community, including the Black-and-white-casqued Hornbill *Bycanistes subcylindricus*, and experience even slightly higher levels of seed dispersal rates in fragments than in main forest sites (see chapter 3). Furthermore, trees standing in fragments were as frequently visited by hornbills than trees in main forest sites.

These results suggest that field observations on visitation and seed dispersal rates in forest fragments might yield quite different results than population genetic analyses. The field observations showed that trees in forest fragments were still as frequently visited and dispersed as trees in main forest sites and suggest that the fragments are still as connected and "healthy" as the main forest sites. In contrast, the genetic data strongly suggest that, nevertheless, gene flow is presently lower than 80-100 years ago and that fragmentation had a negative impact on the genetic diversity of the tree. These results demonstrate that population genetic data are a sensitive indicator of the impact of anthropogenic forest fragmentation on tree populations, and, potentially, more so than field observations on seed dispersers.

How might the discrepancy between field observations and population genetic data be explained? One possibility is that the diversity and abundance of dispersal agents might have been higher 80-100 years ago and has, since, declined. Alternatively, seed dispersers might have changed their movement pattern and, nowadays cover shorter distances than 80-100 years ago. Both hypotheses are difficult to prove. However, they are supported by the fact that genetic differentiation increased not only between the fragments and the main

forest, but also among the four sites within the continuous forest, that are presently as connected as 80-100 years ago.

Finally, the reduced gene flow and increased population differentiation could result from a decline in the density of *P. africana* trees. *Prunus africana* has been heavily logged in the past 70 years (Mitchell 2004) and populations have further declined in the recent past (Fashing 2004). High densities of conspecifics in the past might have promoted extensive gene flow since distances between tree individuals were small and might have been easily covered by pollinators and seed dispersers (Murawski and Hamrick 1992, Young et al. 1996, but see White et al. 2002).

To conclude, my results indicate restricted gene flow in the seedling as compared to the adult generation of *P. africana* as a consequence of recent forest fragmentation of Kakamega Forest. This diminished gene exchange could be caused by reduced seed dispersal. In this case, I found a surprising contradiction between observational data that suggest high visitation and seed dispersal rates of *P. africana* in forest fragments, and the population genetic data that showed restricted gene flow. These results demonstrate that population genetic data are a sensitive indicator concerning the impact of anthropogenic forest fragmentation on tree populations, and, potentially, more so than field observations on pollinators or seed dispersers. Furthermore, my results suggest, that when studying long-lived tree species, sampling different generations, i.e. adults and seedlings, offers the unique opportunity to compare historical and present patterns of gene flow in the trees. This knowledge is essential for developing sound conservation and management strategies not only for tree populations at the landscape scale.

5.5 Summary

Habitat fragmentation can limit gene flow in plants, raising inbreeding and genetic drift in populations and increasing genetic differentiation among populations. However, only few studies have demonstrated that fragmentation caused changes in gene flow over time. I examined the effects of forest fragmentation on the genetic structure of adult trees ($N = 93$) and seedlings (N = 58) of *Prunus africana* in Kakamega Forest, western Kenya, using six microsatellites. Taking samples of adults and seedlings allowed studying changes in gene flow between generations with adults reflecting the pattern before and seedlings after forest fragmentation. I found 98 alleles in the six loci examined, 94 and 73 of them in adults and

seedlings, respectively. Allelic diversity and heterozygosity were significantly lower in seedlings than in adults correcting for sample size. Genetic differentiation of adult trees was very low (overall $F_{ST} = 0.026$) with ~ 97 % of the genetic variation within populations, reflecting extensive gene flow in the past. Genetic variation of seedlings was somewhat higher (overall $F_{ST} = 0.086$) with 24 of the 28 pairwise F_{ST}-values being significantly different from zero, but still ~ 91 % of the variation was within populations. Correspondingly, hierarchical analysis of variance revealed an increase in genetic differentiation among fragmented forests from the adult to the seedling stage (from 0.00 to 2.52 % of variation). Finally, I found no isolation by distance pattern for adults but for seedlings. These results suggest that habitat fragmentation has reduced gene flow in *P. africana* in the past 80-100 years.

6 GENERAL CONCLUSIONS

Anthropogenic forest fragmentation and disturbance are major threats for species diversity, genetic diversity and ecosystem processes. Both biodiversity and processes are vital for the maintenance and conservation of ecosystems. Thus, loss of biodiversity and ecosystem processes may have critical implications for ecosystem functioning. In this thesis I studied the consequences of fragmentation and disturbance for frugivores and seed dispersal, for small mammals and seed predation rates, and for the genetic structure of *Prunus africana* (Rosaceae) populations in western Kenya.

In a first approach (chapter 3) I focused on the frugivore community and seed dispersal of *P. africana* in the heavily fragmented and disturbed Kakamega Forest. I addressed the questions whether fragmentation and disturbance affect the species composition and abundance of the frugivore community of the forest and the frugivore assemblage feeding on *P. africana*. In both objectives I additionally considered the forest dependency of frugivores. Since crop size and fruit availability are known to affect frugivores I determined their influence on frugivores visiting *P. africana*. Moreover, I tested whether seed dispersal rates varied between differently fragmented and between differently disturbed sites. During the frugivore census of the forest I recorded 49 frugivorous bird and monkey species and observed 36 of them feeding on *P. africana* fruits. Even though the overall frugivore species richness of the forest declined marginally significantly from main forest to fragmented sites I recorded slightly higher numbers of frugivores in *P. africana* trees in fragments than in main forest sites. Overall species richness was higher in highly than in less disturbed sites and concordantly significantly increased in *P. africana* trees from less to highly disturbed sites. Correspondingly, seed

dispersal was marginally significantly higher in fragments than in main forest sites and in highly compared to less disturbed sites. In the analyses concerning the different forest dependency groups I revealed similar responses of the groups to fragmentation and disturbance regime. Crop size and fruit availability of surrounding trees affected the number of visitors to some degree. These results suggest that the quantity of seed dispersal seems to be slightly enhanced in fragments and highly disturbed sites, indicating a certain degree of redundancy in an ecosystem which may compensate loss of single species in the short-term.

In a second approach (chapter 4) I studied the consequences of fragmentation and disturbance for the seed predator activity and seed predation rate of *P. africana*. I quantified the activity of small mammals in the main forest, in forest fragments and in differently disturbed sites in the dry and in the rainy season and performed feeding experiments to identify potential seed predators. Moreover, I determined whether fragmentation and disturbance affect the predation rate of *P. africana* seeds. The results suggest that terrestrial predation of *P. africana* seeds in Kakamega Forest was mainly caused by small mammals. I recorded a tendency towards higher activity of seed predators in highly disturbed compared to less disturbed sites in the dry season. Single seeds in contrast to groups of seeds of *P. africana* had significantly higher predation rates in highly disturbed compared to less disturbed sites, again only in the dry season. Whereas the process of seed dispersal seems to be slightly strengthened in fragmented and in heavily disturbed sites in Kakamega Forest, the subsequent process of seed predation trended towards higher predation rates in more heavily disturbed sites. Thus, the two studied processes in the life cycle of *P. africana* are to some degree counteracting demonstrating that extrapolation of the results from one process in the life cycle of a tree to another seem impossible.

In a third approach (chapter 5) I investigated the genetic structure of *P. africana* populations in the main forest and in surrounding fragments of Kakamega Forest using six microsatellite markers. I considered 93 adult trees and 58 seedlings which allows studying changes in the gene flow pattern between stage classes. Adult trees represent a historical pattern of gene flow pre-dating intensive forest fragmentation whereas seedlings mirror the actual pattern strongly influenced by fragmentation. I addressed the questions whether genetic differentiation exists among adult trees and in which way human induced forest fragmentation affects the genetic structure among seedlings. I found a total of 98 alleles in the six examined loci, 94 and 73 of them in adults and seedlings, respectively. Allelic

diversity varied between populations ranging from 37 to 54 in adults and from 15 to 40 in seedlings. Population genetic differentiation of adult trees revealed low $F_{ST} = 0.026$ with ~ 97 % of the variation among individuals within populations, reflecting extensive gene flow in the past. Genetic variation of seedlings was still low ($F_{ST} = 0.086$) with ~ 91 % of the variation within populations. I recorded no IBD-pattern for adults but for seedlings. Increased genetic differentiation combined with the IBD-pattern for seedlings compared to adults are first indicators for restricted gene flow in the seedling stage class as a result of forest fragmentation.

The results obtained in this thesis have important implications for conservation. First, the exemplary study on frugivores and seed dispersal show that human induced fragmentation and disturbance can result in a loss of frugivore species diversity. Surprisingly, the process and service of seed dispersal of *P. africana* was slightly enhanced in fragmented and in disturbed sites indicating a certain degree of redundancy in an ecosystem that may compensate loss of single species in the short-term. Second, the investigation of seed predator activity and seed predation rates revealed a trend towards increasing seed predator activity and in turn enhanced seed predation rates following human disturbance. The results therefore suggest that the regeneration potential of *P. africana* may be reduced even though the quantity of seed dispersal is slightly enhanced. Third, the study on the genetic structure of *P. africana* revealed a decrease of gene flow and consequently an increase of genetic differentiation from adults to seedling caused by habitat fragmentation indicating restriction of pollination and seed dispersal between forest patches.

To conclude, the ascertained reduction of frugivore diversity as a result of fragmentation may for the short-term lead to enhanced quantitative dispersal of single species but can have far-reaching implications for animal-dispersed trees and forest composition in the long-term. Additionally, the increased seed predation rates suggest rather diminished regeneration potential of *P. africana*. This is supported by the results of the genetic structure showing a decline of genetic diversity over time. Thus, the process of seed predation seems to be more responsive to fragmentation and disturbance compared to the seed dispersal service. Moreover, the genetic structure of populations appears to be a more sensitive indicator to the impact of fragmentation than field data on ecosystem processes. Therefore, it is not possible to extrapolate from enhanced seed dispersal rates to increased gene flow. These results highlight the importance of combining studies on

species diversity and ecosystem functioning. Moreover, it is important to investigate several processes in the life cycle of tree species to obtain a complete picture of its regeneration capability. Monitoring of key ecosystem processes and services seems to form an appropriate indicator system of human induced fragmentation and disturbance. Beyond this it is vital to study the level of genetic diversity of species as it provides evolutionary potential for the future. Thus, the combination of these different indicator systems could provide a profound basis for sound management and conservation strategies for single species and ecosystem functioning.

However, to understand the complete regeneration of *P. africana* it would be important to study also its seedling establishment and sapling growth. Moreover, it would be advisable to work in different areas to see whether the obtained results are representative for the species and to study different species to ascertain whether the achieved results are representative for this forest. In the future, compiling data on genetic and species diversity together with data on ecosystem processes and service would allow a deeper understanding of tropical forest ecosystem functioning. Furthermore, considering the ongoing loss of biodiversity in response to human impact, it is pivotal to examine all aspects of community structure and their consequences on functional processes to sustain ecosystems in the long-term.

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